Seed characteristics and resource requirements of broom *(Cytisus scoparius)*, elder *(Sambucus nigra)* and mahoe *(Melicytus ramiflorus)* in the context of a secondary succession

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Abstract

This study investigated the role of the seed characteristics, light, nutrient and water requirements of broom *(Cytisus scoparius),* elder *(Sambucus nigra)* and mahoe *(Melicytus ramiflorus)* in an attempt to clarify the successional sequence of broom through elder to mahoe in the Hoon Hay Valley, Christchurch, New Zealand. The study took a comparative approach under controlled conditions and aimed to understand the factors and/or processes contributing to the dynamics of this successional pathway.

Hoon Hay Valley was once dominated by a conifer/broadleaved forest that was destroyed by both a series of fires and the extensive farming practices of European settlers. The present vegetation is the result of a recovery process that can be described as a secondary succession. The successional pathway from broom through elder to mahoe, proposed by Williams (1983), provided the foundation for the research described in this thesis. Three hypotheses were proposed to test the dependence of the species sequence, in the successional pathway, on differences in the seed characteristics, light, nutrient and water requirements.

Seed weight was significantly different between species with broom being the heaviest and mahoe lightest. An important trend was seen in the contribution of the embryo fraction to the seed weight where broom<elder< mahoe. Broom seeds consistently showed maximum viability with a minimal loss of viability over two years. Elder showed 84% viability when fresh, reduced to 80% after 2 years. Mahoe seed viability was 100% when fresh, yet reduced significantly to 78% over a two year period. Scarification significantly increased the final seed germination of broom. Scarification also significantly increased the rate of germination of both broom and mahoe. Elder did not show any significant effect of scarification on seed germination. Both broom and mahoe were able to germinate in the dark, while elder did not germinate in the dark during the experimental period. Elder required temperature stratification (warm followed by cold stratification, followed or not by a second warm period) for successful (60%) germination. Broom was able to emerge from deeper levels of soil than either elder or mahoe.

Differences in the light requirement of seedlings were clearly demonstrated between species. The light demand for the successful growth of seedlings decreased significantly between species in the order broom>elder>mahoe. For mahoe, nitrogen was found to be a more important limiting resource for growth than different levels of light. Phosphorus significantly affected the growth rate and biomass production of broom, while it had a significant effect only on the height of elder and mahoe.

Broom seedlings were able to grow more successfully under conditions of water stress compared with elder and mahoe. Broom was able to tolerate significantly lower levels of leaf water content than elder and mahoe, without showing signs of wilting. Seedling rooting depths were significantly different between species in the

order of broom>elder>mahoe. Under water stressed conditions, the maximum root penetration of broom was significantly increased. Water use efficiency was significantly different between species, in the order broom>elder>mahoe. Seed germination decreased significantly with increasing water stress in all species. Overall germination was higher in broom than either elder or mahoe under conditions of water stress.

Broom and mahoe appear to have versatile seed characteristics that facilitate arrival and germination, irrespective of light conditions. Broom, especially, maintains an active seed supply in the seed bank for several years. Mahoe showed a considerable decrease in viability over time, indicating the seed bank was relatively unimportant for this species. The need for temperature stratification in elder, limits germination compared to the other species which germinate rapidly irrespective of the pattern of temperature fluctuations. However, in the field conditions, seeds in the persistent soil seed bank face seasonal temperature fluctuations and thereby fulfil the requirement of stratified temperature and can be ready to germinate. The light dependent growth of broom seedlings restrict its establishment under a canopy. Broom may have a better chance of survival under drought conditions (often experienced in exposed sites) due to the ability to function more normally in water limiting conditions, as compared with elder and mahoe. Broom may therefore be regarded as a favoured species for open sites. The study supported the hypotheses that the succession from broom through elder to mahoe is dependent on differences in seed characteristics, light, nutrient and water requirements. The study suggested that the species sequence in the Hoon Hay Valley represented an early to mid successional stage, rather than the earliest stages of succession as postulated by Williams (1983).

Chapter 1

General Introduction

1.1. Introduction

Succession generally refers to the changes observed in an ecological community following a disturbance (Connell and Slatyer 1977). These changes may include species replacement, shifts in population structure and changes in the availability of resources (Luken 1990). Clements (1916) provided one of the earliest descriptions to explain succession and identified six processes which operate during succession. They are (i) *nudation*, the creation of bare soil to start the succession; (ii) *migration*, the arrival of propagules from elsewhere (or those remaining in the soil); (iii) *ecesis*, successful establishment; (iv) *competition*, the interactions of species for limiting resources; (v) *reaction*, the response of the environment as a result of growth, death and changing resource availability; and (vi) *stabilisation*, where the most suitable species establish at the site. Plant succession has also been explained in terms of the importance of the propagule pool (Egler 1954) and the sorting of species along resource gradients as a result of competition (Drury and Nisbet 1973; Pickett 1976). A three phase model for succession involving facilitation, tolerance and inhibition was suggested by Connell and Slatyer (1977). Tilman (1980, 1982) emphasized the resource requirements of the species and the supply rate of resources as deciding factors of the outcome of the competition between species.

Despite the rich literature on plant succession, this complex process is still poorly understood and difficult to predict (Luken 1990). McIntosh (1980) noted succession to be "one of the oldest, most basic, yet still in some ways, most confounded of ecological concepts".

Ecological restoration can be considered as the human effort to copy natural succession and ever-increasing habitat degradation has led to a surge of interest in restoration (Bradshaw 1983). The study of ecological succession is important because the knowledge gathered from such studies can be used in directing the restoration of degraded and/or disturbed land. Restoration involves an acceleration of the natural successional processes in order to return a landscape to a more highly developed state (Sauser 1998). Although there are different views in the definition, goal-setting and methodologies used to achieve restoration, the objectives are basically the same. Restoration may be carried out to improve productive capacity, to enhance conservation values in protected or productive landscapes, or to restore localized, highly degraded sites (Hobbs and Norton 1996). Restoration has become an important component of conservation, with a number of direct benefits flowing on to biodiversity. It can be useful in the provision of additional habitats and may enable linkage of isolated remnants through restored corridors (Hobbs 1992, 1993; Murcia 1995).

The effective restoration of disturbed sites is dependent on an understanding of the distinctive characteristics and management needs of key species in such successions. The restoration of degraded ecosystems is regarded as an important conservation strategy in New Zealand because of the substantial human-mediated alteration of both mainland and offshore island ecosystems. A number of restoration projects have been undertaken in New Zealand (Atkinson 1988; Chester and Raine 1990). The Hoon Hay Valley restoration is one of several ongoing restoration projects underway on Banks Peninsula.

The Hoon Hay Valley (occupying an area of approximately 400 ha) lies on the western flanks of the Port Hills of Canterbury in New Zealand's South Island. The

original forest vegetation in the valley was dominated by matai *(Prumnopitys taxifolia)*, kahikatea *(Dacrycarpus dacrydioides)* and totara *(Podocarpus totara)* (Ogilvie 1978). The arrival of Europeans and their farming systems (Partridge 1992) together with extensive fires, especially in 1868 (Ogilvie 1978), greatly reduced the forest cover. A mosaic of vegetation types has resulted from these disturbances and the valley is presently undergoing different stages of secondary succession.

Several research studies have been undertaken on aspects of ecosystem change in the Hoon Hay Valley, and the immediately adjacent areas of Banks Peninsula (Griffiths 1974; Williams 1983; Jayet 1986; Partridge 1989, 1992; Burrows 1994a, b, c; Cullen 1996; Reay 1996; O'Cain 1997; Dungan 1997; Reay and Norton 1999a, b). Based on an investigation of the vegetation structure and composition of successional scrub in Hoon Hay Valley, Williams (1983) postulated a possible successional pathway from broom *(Cytisus scoparius)* through elder *(Sambucus nigra)* to mahoe *(Melicytus ramiflorus)*. Although this broom→ elder→ mahoe succession has also been supported by Dungan (1997), no detailed study has been undertaken on the factors and/or processes that contribute to the successional dynamics. This successional pathway forms the basis of the research presented in this thesis. A comparative study of seed characteristics, light, nutrient and water requirements of broom, elder and mahoe is described and analysed in order to better understand the dynamics of this successional pattern.

1.2. Aim and the focus of the research

Successful restoration must be based on an understanding of the ecology of natural ecosystems and processes. Many different points of view can be used in the study of successional relationships, as it is an exceedingly complex process involving the whole ecosystem (Bazzaz 1990). In order to simplify the complexity, one approach is to focus on one specific pathway at a time and learn as much about it as possible. The research reported in this thesis focuses on one already-proposed successional pathway in detail and aims to understand the factors that control the dynamics of the

pathway. The study considers three key factors that may be important in the establishment and early growth of plants in an ecosystem. These are seed characteristics, light, nutrient and water requirements.

1.3. The comparative approach

An understanding of the processes that control the structure and composition of vegetation can be derived from three types of research; correlative, direct and comparative (Grime 1979). The correlative approach explains variation in vegetation composition by reference to associated environmental variations. The direct approach deals with the observation and recording of the establishment, longevity and reproduction of individual plants in natural vegetation at specific field sites. The comparative approach involves the study of germination, growth and the reproductive physiology of a species under standardized experimental conditions (Grime 1979). The present research has adopted the comparative approach described by Grime (1979). As the successional sequence proposed by Williams (1983) was based on field observations (by direct approach), a comparative study under controlled conditions would be expected to enhance our current understanding and interpretation of this proposed successional pathway.

The principal aim in designing experiments under controlled conditions is to test for the effects of a single, or a small number of factors at a time while maintaining all others at a constant level. Plants in the field grow under conditions which are changing continuously, in microclimates which are spatially dense and in communities in which individuals interact with one another.

1.4. Research objectives

The primary objective of this research was to determine the processes and mechanisms involved in the succession of broom through elder to mahoe. Within this primary objective were three secondary objectives, to examine the influence of:

i) seed characteristics;
ii) light and nutrient requirements;
iii) water requirements;

in the observed successional sequence.

The research outcomes were expected to,

i) Verify the proposed successional sequence of broom→elder→mahoe by a study under controlled conditions.

ii) Contribute to the understanding of processes involved in vegetation succession by a consideration of the three plant species in detail.

iii) Emphasise the role and/or importance of broom, elder and mahoe, in a secondary succession.

1.5. Thesis structure

The thesis consists of seven chapters. Chapter 1 introduces and justifies the research. Chapter 2 reviews the relevant literature. Chapter 3 provides general descriptions of the three investigated plant species. Chapters 4, 5 and 6 deal with experiments on the seed characteristics, light, nutrient and water requirements of broom, elder and mahoe. Each of the experiments in those chapters are presented separately. Chapter 7

summarizes and discusses the results, with respect to the hypotheses presented at the beginning of the research. Figure 1.1 illustrates the structure of the thesis.

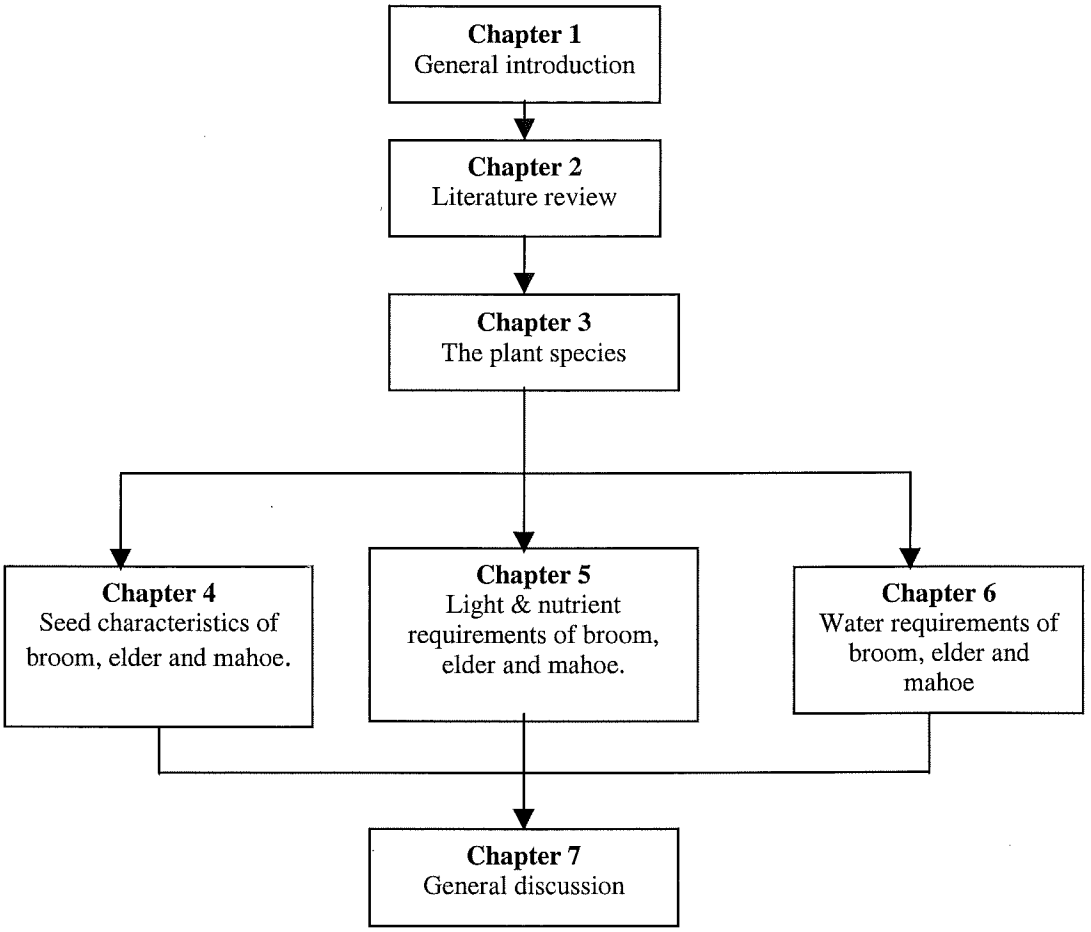


Figure 1.1. Diagrammatic representation of the thesis structure.

Chapter 2

Literature review

2.1. Introduction

This chapter provides background for the research by reviewing the related literature. The importance of restoration for conservation is discussed, goals are defined, and restoration examples from both around the world and New Zealand are presented. The importance of the study of succession is emphasized in considering succession as a model for restoration. This is followed by a discussion of the processes and theories of ecosystem succession. Seed characteristics, light, nutrient and water requirements of the plant species, in relation to succession, are reviewed. A description of Hoon Hay Valley is provided and the successional sequence postulated by Williams (1983) is presented. The research hypotheses are then stated.

2.2. The restoration of disturbed ecosystems

2.2.1. Disturbance and the need for restoration

All living organisms are dependent on their environment for survival. According to Dubos (1976), earth should be seen *'neither as an ecosystem to be preserved unchanged nor as a quarry to be exploited for selfish and short-range economic reasons, but as a garden to be cultivated for the development of its own potentialities of the human adventure'*. This quote emphasizes the degree of mutual dependence between earth and humanity.

Prior to the industrial revolution, when the total human population was much lower than at present, resources were apparently abundant and their utilization was not seen

to compromise ecosystems greatly. However, a rapidly increasing human population demanded more from the environment, leading to extensive and intensive resource exploitation. For example, the industrial revolution has led to the exploitation of natural resources in order to provide a better quality of life and additional comfort for humans. Moreover, human wars intensified ecosystem disturbances in the 20 th century.

Wali (1987) defined ecosystem disturbance as an event, or series of events, that result in changing the relationship of organisms and their habitats from their natural state, both spatially and temporally.

Ecosystem disturbances are basically of two types, natural or anthropogenic. Natural disturbances include volcanic activity, earthquakes, floods, meteor strikes, windstorms, fire, landslides and insect outbreaks (Wali 1992a). Anthropogenic disturbances tend to have temporally narrow, but spatially wide, impacts on ecosystems (Wali 1992a). Such disturbances may include (i) extensive clearing of natural vegetation (ii) selective harvesting of desirable species, (iii) introduction of undesirable species alien to a given area, (iv) abandonment of unproductive agricultural land, (v) mining and improper reclamation of mined lands, (vi) introduction of biocides and other chemicals to the environment and (vii) war, which affects ecosystems by bombing, defoliation and movement of people and material (Bazzaz 1983). Many of these disturbances have widespread effects and very few places in the world remain untouched (Wali 1992a,b). The restoration of over-exploited ecosystems has become an urgent need.

2.2.2. Defining restoration

Reclamation, rehabilitation, and restoration are terms used to describe the renewal, repair and re-establishment of degraded ecosystems. The United States National Research Council (USNRC) (1974) recognized a need for uniformity in terminology because consistency in terminology helps development and acceptance of the initial criterion of a discipline (Kuhn 1970). Restoration implies the conditions of the site at

the time of disturbance will be replicated after a developmental activity. According to the Society of Ecological Restoration, restoration is an intentional alteration of a site to establish a defined indigenous, historic ecosystem to emulate the structure, function, diversity, and dynamics of the specific ecosystem (Aronson *et al.* 1993). Rehabilitation returns the land to a form and productivity outlined in an approved land use plan, which ensures the system is economically stable, does not contribute to environmental deterioration and is constant with the surrounding aesthetic values and resembles restoration by adopting indigenous ecosystem's structure and functioning as guidelines to follow (USNRC 1974; Aronson *et al.* 1993). Rehabilitation is often called as reclamation, refers to the modification of a site back to a habitable status for organisms that were originally present, or for others that approximate the original inhabitants (USNRC (1974).

There remains some ambiguity in relation to the naturalness and full value of restored ecosystems (Gunn 1991; Elliot 1994), often hindering the progress of the science (Simberloff 1990). For example, both Magnuson *et al.* (1980) and Morrison (1987) defined restoration as producing exactly the community or ecosystem that was previously present. This seems to be impossible in an ever-changing real world. Atkinson (1988) defined restoration as active intervention and management to restore biotic communities that were formerly present at a particular place and time. Hobbs and Norton (1996) further developed this definition as '*the active intervention and management to restore or partially restore biotic communities, both their plants and animals, and the associated physical environment as fully functioning and sustainable systems with a predominance of indigenous species*'.

2.2.3. Restoration goals

Clearly defined goals are essential to any research program, including ecological restoration. Although restoration has received marked interest amongst researchers, goals are often argued or debated. Daily (1993) suggested that the restoration of ecosystems to pre-disturbance conditions is generally not a viable goal because the

sequence of events that lead to the development of any particular ecosystem would be impossible to replicate exactly. Cairns (1989) supported this view mentioning that restoration efforts to create pre-disturbance conditions are not feasible because the sequence of events leading to the development of any particular ecosystem is unique and would be impossible to replicate.

Daily (1993) discussed the social constraints of restoration stating that restoration goals should be set by taking a nation's particular status (social, economic, political and biological factors) into consideration. Daily (1993) further suggested that, in developed nations the goal should be to create a self-sustaining ecosystem that has structure and functions similar to those of the pre-disturbance system, enabling eventual integration into the ecological landscape. In developing nations, restoration goals often include direct economic benefits from the restored land.

Elliot (1994) claimed that the full value of an ecosystem cannot be restored even if the results of a restoration project were indistinguishable from the original ecosystem, as a restored environment is not naturally evolved and it lacks an unbroken history. In contrast, Gunn (1991) maintains that it is possible to restore degraded natural systems to their full value if distinctive species are extant.

It is however, important to set realistic and pragmatic goals for restoration. The primary goal of a restoration program should be to restore a site to an ecologically functioning condition similar to other comparable sites with both components (a certain set of plant and animal species) and interactions (processes that are necessary to maintain the system) present (Norton 1993).

2.2.4. The importance of ecological restoration

Restoration ecology is receiving attention from the scientific community, due to the urgent need to recover damaged and degraded ecosystems. Hobbs (1993) discussed

three main ways in which restoration can be useful. He suggested that restoration activities can: (i) create buffer zones to protect existing remnants from edge effects (ii) form corridors to increase relationships and connections between remnants (iii) result in additional habitats to increase the effective size of the remnants. The development of corridors can also be useful in linking previously isolated remnants (Hobbs 1992) and providing buffers to lessen the effect of external factors (Murcia 1995). Restoration is a useful tool for dealing with highly degraded sites, such as mines, by enabling the integration of non-productive land-use systems with adjacent unmodified vegetation (Norton 1991).

The benefits of ecological restoration are both short-term and long-term (Towns *et al.* 1990). In the short-term, restoration may lower the vulnerability of threatened species and decrease dangers to threatened communities, while in the long term, restoration can re-establish lost trophic links in ecosystems, thus restoring the natural processes of evolution (Towns *et al.* 1990). Restoration can be useful in decreasing the rate of global decline in biodiversity. Species extinction is a part of natural evolution; species that do not fit into the environment eventually disappear from ecosystems. However, in the past 400 years, at least 63 mammal and 88 bird species have become extinct through human activities (Diamond 1986). Currently, nearly 10% of the world's plant species are threatened (Prance 1991). This accelerated loss of species has prompted the urgency to both understand and undertake restoration activities.

Restoration provides an opportunity to test our understanding of ecosystem development and functioning as we attempt to artificially conquer the factors that we consider may restrict ecosystem development (Bradshaw 1987a). Further more, co-ordination and co-operation with public groups in restoration endeavors to keep local communities informed about nature and conservation (Bellingham 1990).

Restoration is also an important tool for increasing the productive values of ecosystems and therefore can be used as an option for integrating production and

conservation. For instance, restoration projects can be targeted to deal with soil salinity problems (Norton 1994).

2.2.5. The restoration process

The process of restoration involves the conversion of a degraded site to a state similar to that, which would have occurred had the disturbance not taken place. In natural systems this process is normally achieved by succession over a long period of time. Restoration projects try to accelerate the natural process of succession.

To restore degraded biotic communities back to fully functioning systems, Atkinson (1988) outlined three essential ingredients; a restoration goal, active intervention, and monitoring of progress. The establishment of communities in degraded sites requires a clear set of objectives and a realistic appraisal of what is achievable. Beeby (1993) suggested four factors need to be considered in developing objectives for community establishment; (i) a capacity to restore, in order to identify realistic prospects of recreating the original system, (ii) the financial constraints and availability of resources such as soil, water and litter, (iii) local ecological, social or economic needs, and (iv) pollution pressure on surrounding areas.

Any restoration project essentially has two stages, to discover and understand what is wrong, and to appropriately reverse the degradation (Bradshaw 1987b). The first stage is as important as the second, because what is done in the second stage must result from what was discovered in the first stage. These two stages require a detailed understanding of the nature of the ecosystem, the nature of the damage and how to repair the damage (Bradshaw 1987b). Ecosystem restoration is essentially an experiment testing an ecologist's understanding of ecosystems (Bradshaw 1987a).

Ecosystem development can be quantified in two dimensions; structure and function. When ecosystems are degraded, both these dimensions reduce in terms of complexity

and naturalness, while during the process of succession there is an increase in both dimensions (Bradshaw 1984). A number of methods can be used to identify what is wrong in an ecosystem, depending on the site and circumstances. The structure of the present site vegetation can be measured in terms of species diversity, and the physical and biological complexity, while its functions are measured in terms of processes (Bradshaw 1987b). For example, Miyawaki (1992) undertook a vegetation survey examining the ecology and phyto-sociology to identify species diversity and complexity prior to the formulation of a scheme to restore a natural forest in Japan.

In addition, one must not underestimate the animal component of an ecosystem as animals are important as dispersal agents of plant propagules (Brenner and Kelly 1981). Soil surveys are equally important because of their physical and nutritional interactions with plants. Determining the intensity and scale of ecosystem disruption will enable the formulation of an appropriate restoration plan.

The work required in a restoration program is dependent on a number of factors including the degree of damage, the objective of the restoration activity and the resources available, including finance and conditions of the site (Schaller and Sutton 1978; Bradshaw and Chadwick 1980; Sauser 1998). Possible activities involved in a restoration program are summarized in Figure 2.1. The type of research describe in this thesis would fit into Figure 2.1 by providing useful information on key species of the investigation. This can help the formulation of appropriate strategies for a restoration project, to improve the recovery process, especially plant species recovery.

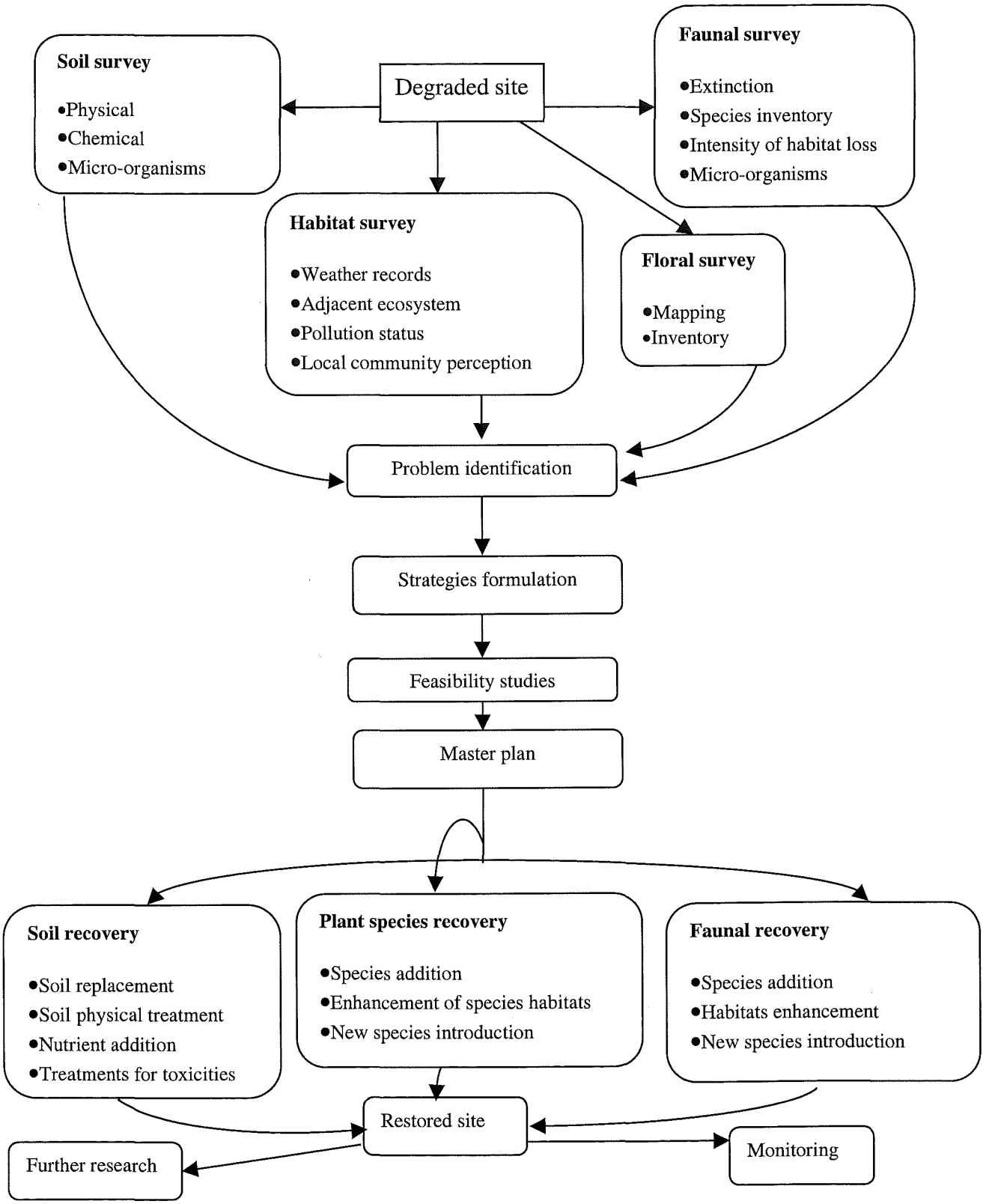


Figure 2.1. Summary of the possible activities in a restoration project. (Based on information from Schaller and Sutton 1978; Bradshaw and Chadwick 1980; Sauser 1998)

Attempting ecological restoration is a positive action irrespective of its level of success. When a restoration project fails, we gain insights into how ecosystems work, provided the cause for the failure is determined (Ewel 1987). However, this can be expensive in terms of wasted resources and may result in people developing a negative attitude towards restoration. On the other hand, when a restoration project is successful, a degraded site is developed to a state comparable to what might have been prior to the disturbance (Ewel 1987) often receiving considerable public support.

Measuring success is another issue in a restoration activity. A number of criteria can be used to measure the success of restoration projects. Simberloff (1990) suggests that a restoration can be considered fully successful if it provides a system whose structure and function cannot be shown to be outside the bounds generated by the normal dynamic processes of communities and ecosystems. Atkinson (1990) suggested the recovery of individual species, replacement of extinct species, or extinct taxa and the establishment of self-maintaining populations of species were useful criteria to measure success. Success, measured either by the resemblance of the reconstituted community to the original, or whether it has the same species and a similar physiognomy, are superficial comparisons as they are often deceptive in the longer term because of the disintegration of the restored community (Ewel 1987). He suggested five criteria could be used to judge the level of success of a restored system; (i) *sustainability* (whether the restored community is capable of perpetuating itself); (ii) *invasibility* (whether the restored community can resist invasions by new species, easily invadiable communities are given less ranking in measuring success because invasions are symptoms of incomplete use of light water and nutrients); (iii) *productivity* (whether the restored system is as productive as the original); (iv) *nutrient retention* (whether the restored system loses greater amounts of nutrients than the original) and (v) *biotic interactions* (whether the restored system resembles the original system plant and animal communities). However, it is difficult to compare a restored system to an original that no longer exists. Reay and Norton (1999b) assessed restoration success by investigating the flora and ground invertebrate fauna of different-aged restoration plantings. In measuring success they

looked at the colonization of indigenous flora and invertebrate fauna, species selection in relation to initial colonization, the role of fruiting tree species in attracting seed-dispersing birds, ecosystem structure, function and successional sequences.

2.2.6. Restoration examples

The literature is rich with examples of restoration (e.g. Merton 1972; Fullager 1978; Wingate 1978; Wingate 1985; Hermes *et al.* 1986; Janzen 1986). Restoration projects can involve either the re-establishment of a few species (where biotic communities had been partly damaged) or projects where the majority of indigenous plants and animal species had been lost (Atkinson 1988). Successful restoration projects have been undertaken in Guanacaste National Park, Costa Rica, Phillip Island in the Pacific Ocean, Round Island in the Indian Ocean and Nonsuch Island in the Atlantic Ocean; these projects involved major work in re-establishing plant and animal communities (Atkinson 1988). The Guanacaste National Park restoration project in Costa Rica was carried out in an area of 700 km^2 with an aim to conserve 30000 insect species, 3000 plant species, 500 bird species, 200 reptile and amphibian species and 160 mammal species; it was also successful in attracting strong national support through educational, scientific and management activities (Janzen 1986).

On Phillip Island in the Pacific Ocean, at least 12 native vascular plants appeared to be extinct (Fullager 1978). Following the removal of rabbits by the Australian National Park and Wildlife Service in 1986 (Hermes *et al.* 1986), some endemic plants not previously seen were discovered in reasonable numbers (Atkinson 1988). The island is now free of introduced mammals and the re-establishment of many common woody plant species has been successful (Atkinson 1988).

2.2.7. Restoration efforts in New Zealand

Human activities on both the main and off-shore islands of New Zealand have devastated much of the endemic vegetation (Mansfield 1996). The biological wealth of New Zealand includes both endemic species and the species once occurred on the mainland but survive now only on islands (pseudo-endemic species) (Daugherty *et al.* 1990). These species are important not only for cultural, aesthetic and scientific reasons but also hold regional, national and international significance.

The Department of Conservation, established by the Conservation Act 1987, is the body responsible for managing the biological heritage of New Zealand on public conservation lands. The restoration of degraded ecosystems is a major conservation strategy in New Zealand and restoration projects are an important part of the Department of Conservation's management goals.

A replanting program on Tiritiri Matangi Island in the Hauraki Gulf is hoping to speed up natural regeneration processes in order to restore forest cover on this island of 222 ha; the success rates of the project have been reported to be as high as 50-80% (Norton 1993). On Mana Island, off the Kapiti Coast, pre-settlement vegetation patterns have been used to assist with a re-vegetation program (Chester and Raine 1990). The Mangere Island project (113 ha) launched in 1974, was expected to be the only way in which the black robin could be saved from extinction (Atkinson 1988). This project involved planting *Olearia traversii* to reduce the effect of high winds, but insufficient monitoring and an under-estimation of climatic conditions resulted in an early but temporary failure, leading to slow growth in the main planting area. On the Mercury Islands, off the eastern Coromandel Peninsula, the reconstruction of lost communities would i) lower the vulnerability of threatened species to extinction ii) decrease the threats to rare communities and iii) re-establish lost trophic links in the ecosystem (Towns *et al.* 1990).

Several projects have also been undertaken on the main islands of New Zealand with a primary goal being to restore a forest composition similar to that which might have occurred prior to human disturbance. Examples include the Porter's Pass project, Matawai Park (Rangiora), Cockayne Reserve (Christchurch), Hinewai Reserve (Banks Peninsula) and Keebles Bush (Manawatu lowlands) (Atkinson 1988). Restoration work in a limestone quarry at Cape Foulwind is aiming to establish a mosaic of indigenous forest and wetland communities on the basis of natural regeneration patterns (Norton 1994). Restoration activities at Pyramid Valley, Brooklands Lagoon and Hoon Hay Reserve have already started or are at the planning stage (Norton 1993).

2.2.7.1. The Hoon Hay Valley restoration ecology project

The Hoon Hay Valley is privately owned as part of the Scott Estate and is now undergoing vegetation recovery following extensive disturbance through grazing and fire. The main aim of the research in the Hoon Hay Valley is to better understand the processes of forest regeneration and its facilitation through ecological restoration. The long term goal is to enhance the return of the Hoon Hay Valley to a vegetation cover dominated by indigenous woody species (Norton 1995). The restoration project, involving co-ordinated research in three overlapping phases, is outlined below.

i) Collection of baseline information on the physical and biological environments

Baseline characterization of the site includes collecting data on vegetation patterns, soil, climate, vertebrate and invertebrate populations. This information provides not only a useful management tool but also is an aid in selecting sites for further research (Norton 1995).

ii) Establishment of long term monitoring programmes

To understand the temporal changes which are occurring as part of succession processes in the Valley, long term research is needed. The variables to be included in the long term monitoring are aspects of vegetation composition and structure, animal community and composition, climate and catchment hydrology (Norton 1995).

iii) Focused research on the ecological basis of forest regeneration and restoration.

This phase of the project involves planned research addressing specific questions on management and theoretical aspects of both technical and ecological research. Technical research looks at maintaining and enhancing regeneration and restoration. Research possibilities include plant propagation and growth, weed and herbivore control. Ecological research examines the mechanisms and processes of regeneration and restoration ecology using an experimental or comparative approach (Norton 1995). The research described in this thesis uses a comparative approach to focus on one specific successional sequence.

2.2.8. The study of natural succession as a model for restoration

Ecosystems transform naturally over a long period of time following a disturbance and restoration is an acceleration of the natural successional process. The basic principles of ecosystem restoration and ecological succession are the same (Bradshaw 1987a). Knowledge of the functioning of natural ecosystems, factors and/or processes involved in natural succession should facilitate the success of any restoration process; the objective of succession research should enable the prediction of changes in vegetation or the effects of altered management (Miles 1987). Concurrent empirical and correlative studies may provide an understanding of how a particular system works, thereby enabling predictions to be made about that ecosystem (Miles 1987).

'..when we experiment in planting forests, we find ourselves at last doing as nature does. Would it not be well to consult with nature in the onset? For she is the most extensive and experienced planter of all.....

Thoreau, H.D.

2.3. Mechanisms underlying succession

Succession is the gradual replacement of short-lived opportunist species with longer-lived competitive species, reflecting an increase in the durational stability of the habitat (Tilman 1988). Successions may be primary or secondary. Primary succession occurs where there is no organic material for colonizing species to exploit. Secondary succession occurs where some pre-disturbance organic component and/or propagules remain (Beeby 1993).

Literature provides evidence of the early enthusiasm for ecological theories of the cause, effect and sequence of species arrival during succession. (e.g. Cowles 1899; Cooper 1913; Clements 1916; Gleason 1917). Clement's theory led the subject for many years because of its simplicity and completeness (Tilman 1982), although it later faced criticism (Gleason 1927; Egler 1954). Successional mechanisms were also examined by Egler (1954), Horn (1976), Whittaker and Levin (1977) and Connell and Slatyer (1977).

Valk (1981) identified three characteristic life-history features of a single species in relation to population dynamics during succession; (i) the life-span of the individual (ii) propagule longevity and (iii) the requirements for propagule establishment. Lawton (1987) argued that species interactions contribute most in determining the patterns and rates of succession rather than life-histories of individual species. He further noted that this aspect of successional dynamics was poorly understood. Noble and Slatyer (1978) also raised the need to study interactions between species in order to predict species replacement during succession. More recently, a number of models have been developed, based on the chances of one species being replaced

by another, and on growth and population data, to predict a community composition that compares well with existing climax communities (e.g. Grime 1977; Connell and Slatyer 1977; Bormann & Likens 1979; Horn 1976; Tilman 1982, 1988; Lawton 1987; Case 1990).

Grime's (1977) theory suggested three primary strategies (competitive, stress tolerant and ruderal) were associated with the morphological features, resource allocation, phenology and response to stress of plants. His model for vegetation succession assumes variation in the relative importance of competition, stress and disturbance as determinants of vegetation succession.

Connell and Slatyer's (1977) model, which was based on possible direct and indirect interactions in an ecosystem, received much attention; their mechanisms and terminology remain widely used by the ecological community today. Three tentative models were suggested to explain the mechanisms of the sequence of species arrival: facilitation, inhibition and tolerance. *Facilitation* suggests that a resident species makes possible, or accelerates, the establishment of colonizing species by virtue of its presence or its effect on the habitat. *Inhibition* suggests the resident species prevent or slow down colonization by new species. *Tolerance* suggests late successional species are able to cope with lower levels of resources. In a successional process, some combination of all these interactions occurs either simultaneously or separately. Facilitation is a more typical interaction type in primary succession; for example, inert mineral soils require enhanced biological activity before higher plants can successfully invade. Inhibition and tolerance have greater significance in secondary succession because species interactions are dominated by existing resources and species (Connell and Slatyer 1977).

Tilman (1988) described two different processes that play a major role in determining which species are abundant at a particular time during the dynamics of secondary succession. They are (i) transient dynamics that are influenced by

maximal growth rates, allocation patterns and the initial availability of resources and (ii) the process of long-term soil change.

Tilman (1988) explained a theory of plant competition for resources and gave a realistic model of the mechanism for competitive displacement of species. This model assumes when several species compete for the same resource, a competitive displacement of species occurs through depression of resource availability. When several species compete for a single limiting resource, Tilman's theory predicts that the species with lower R* (the amount of resources needed to maintain a stable equilibrium population for a particular species) should be competitively dominant, depending on initial densities.

When species compete for two or more resources, the requirement for resources is represented by resource-dependent growth isoclines (Tilman 1982) The theory predicts that if the zero net growth isoclines of two species do not cross, the species with the lower requirement for the resources should competitively displace the other species. If the isoclines cross, the point at which they cross is the equilibrium point, the point of coexistence. Inter-specific competition results in replacement of one species by the other or coexistence.

According to allocation pattern and life history theory, energy allocation to roots, leaves and stems can greatly influence the maximal growth rates and competitive abilities of a plant (Tilman 1988). Individuals with a higher energy allocation to roots can survive at lower soil nutrient levels than individuals that allocate more to leaves and stems. Allocation to both leaves and stems influences the ability of an individual to survive in habitats with low light intensity at the soil surface.

The colonization and competitive abilities of species, versus their susceptibility to herbivory, are also important determinants of successional patterns. Two hypotheses have been proposed (Tilman 1988). The *colonization-competition hypothesis*, which assumes that better colonizing species are poor competitors and as a result, disturbed

sites are gradually invaded by poorer colonists but superior competitors. Such sites would ultimately be dominated by the species that are poorest colonizers but the best competitors. The *colonization-herbivory hypothesis* suggests that good colonists are more sensitive to herbivory and may be displaced by later colonists that are more resistant to herbivory. The importance of colonization, as a determinant of succession increases with increasing nutrient richness. On nutrient rich sites, initial colonists can gain a period of dominance before other better-suited species arrive.

Tilman's (1988) explanation for the pattern of succession determined by competitive abilities of species was based on the *competition-herbivory hypothesis*. This assumes a trade-off in the competitive abilities of species verses their susceptibility to herbivory, with superior competitors being more susceptible. For example, if herbivory increases from low to high during succession, the species sequences would be from good competitors (susceptible to herbivory) to species that are poor competitors (but resistant to herbivory). Successional dynamics are influenced by many processes; including colonization, competition, transient dynamics, herbivory and the relative importance of these processes often determine the outcome (Tilman 1988). Ecological mechanisms are complex and a multiplicity of explanations should be considered because there is not one universal truth (Hills and Vankat 1982).

2.4. Seed characteristics, light, nutrient and water requirements, as factors influencing successional dynamics

The orthodox theory on sequential replacement of species in secondary succession begins with the arrival and colonization of species that are suited to the disturbed site. The modified conditions become more favorable for other late-colonizing species; competition occurs between late-arrival species and resident species resulting in replacement; invasion and replacement continue until no more species are capable of invading the established community (Burrows 1990). The causes of the sequential replacement of species are not easily generalized, as each species has unique physiological, morphological and life history characteristics and each habitat has a unique substrate, geomorphology, climate and past history (Tilman 1988).

Species composition and their sequential replacement during succession, is governed by the key factors of seed characteristics, light, nutrient and water requirements, the relative importance of which alters as a result of changing resource availability during succession (Tilman 1982, 1988; Burrows 1990).

Seed characteristics

Plant species most often enter the process of succession as seeds and can arrive at any time, but, their entry, germination and establishment is either facilitated or inhibited by the vegetation already present (Fenner 1987) or by the conditions of the site. Only seeds of species which have characteristics suited to the present environmental conditions can establish successfully. Therefore, in a vegetation succession, where the species composition and site characteristics are dynamic, the seed properties of successful species are likely to be different according to successional status. Examining the seed characteristics of different species that are dominant at different stages of a succession may help to explain the sequence of floristic changes during succession (Fenner 1987).

Among the seed characteristics that are important in influencing successional sequences are seed size, dispersal modes, and germination requirements (Werner and Platt 1976; Fenner 1985, 1987, 1992; Silvertown 1987; Tilman 1988; Halpern *et al.* 1990; Nakashizuka *et al.* 1993).

Light and nutrients.

Light and nutrients are two important resources likely to change during the course of succession (Tilman 1988; Burrows 1990). While different habitats vary in their ability to provide specific resources, different species display variation in their specific resource requirements. For example, secondary successions on rich soil begin with a high availability of both light and nutrients, while secondary

successions on poor soils start with high light and low nutrients (Tilman 1988). In general, the amount of light reaching the soil surface is increased after a disturbance and reduces with succession (Vitousek and Walker 1987). Bazzaz (1987) reported that early successional species were able to survive over a broader range of nutrient availability than middle and late successional species. As a first step in understanding successional sequences, it is important to determine the light and nutrient requirements of colonizing species.

Water requirements

Water inputs are independent of succession although redistribution and infiltration rates are likely to change with increasing plant cover. Disturbance greatly reduces transpiration and increases evaporation from the soil surface, although the water-holding capacity of the soil varies less in secondary succession compared with primary successions (Vitousek and Walker 1987). Disturbed sites tend to have a drier soil surface and elevated water table although this can vary considerably depending on the nature of the individual site. Varying degrees of water stress conditions occur during succession and species present at different successional stages probably have different levels of tolerance and mechanisms to cope with stress. For example, germinating seeds are very vulnerable to water stress (Harper 1977); species that germinate soon after a disturbance may have an enhanced ability to germinate under a certain level of water stress or cope better with repeated wetting and drying. At the seedling stage early successional species may be able to use water more efficiently, thereby compensating during periods of reduced water availability. Changes within the physical environment (e.g. water, nutrients, air temperature) along successional gradients have received attention by researchers (Bazzaz 1987). An understanding of the processes governing successional sequences would be enhanced by an examination of the water requirements of species which are part of that sequence.

2.5. Hoon Hay Valley

The rationale for this research comes from Williams' (1983) identification of a successional sequence in the Hoon Hay Valley and therefore a description of the area is important.

2.5.1. Location

Hoon Hay Valley is located within the Port Hills Ecological District and lies on the north western flanks of Banks Peninsula, 6 km south of Christchurch, New Zealand. The valley stretches across an altitudinal range from approximately 50 m above sea level to an altitude of 500 m on the upper flanks. The valley covers approximately 400 ha.

2.5.2. Soils

The soils in the valley have been described in four series on the basis of initial mineral material and climate. They have been formed from volcanic deposits, primary loess from the Plains river valleys and related colluvial complexes (Fitzgerald 1966; Griffiths 1974). The Takahe series is derived from loess soils, and the Cashmere series is formed from a basalt matrix. These are found in the sub-humid climate, at elevations less than 300 m. The Summit series and Rapaki series are found above 300 m elevation and are formed from loess soils and basalt soils respectively.

Soils in the valley are well drained and often dry to wilting point in summer. Fertility ranges from medium to good, depending on the parent material. The Rapaki and Cashmere soil series are more fertile than the Takahe and Summit series (Fitzgerald 1966; Griffiths 1974; McClaren and Cameron 1990). Soils are moderately acid, with

a pH of approximately 5.5; they are low in available phosphorus and have moderate amounts of exchangeable cations (Williams 1983).

2.5.3. Climate

The Hoon Hay Valley is classified in the Lowland Bio-climatic zone (Wilson 1993). Its climate is different from the surrounding plains due to the maritime influence of Banks Peninsula and the interactions of winds through the local topographic modification of prevailing air flows (Cullen 1996; Jayet 1986).

The plains immediately adjacent to the Port Hills receive less than 700 mm rain fall annually (Jayet 1986). Griffiths (1974) estimated precipitation at the lower slopes of 760 mm per year and at elevations over 300 m, over 1000 mm per year. Altitude is the most important factor controlling precipitation in the Valley (Cullen 1996). He found that, lower areas and upper areas of the Valley received 36% and 22% more precipitation respectively than the nearest collecting station at Christchurch Airport.

The Valley experiences a slightly lower (1 degree) mean annual temperature than the 11.6 ^{0}C mean annual temperature recorded at the Christchurch airport Cullen (1996). The higher altitudes of the valley experience lower temperatures than the lower altitudes (Cullen 1996).

2.5.4. Vegetation history

Prior to human settlement, the Canterbury plains, Banks Peninsula and Port Hills were predominantly covered by forest (Molloy 1969; Molloy *et al.* 1963; Wilson 1992). The soil profiles commonly associated with forest vegetation in areas currently lacking forest cover strongly suggest an earlier forested landscape (Petrie 1963).

The first human settlement of New Zealand occurred some 1000 years ago (Salmon 1975), although other literature gives notably earlier time scales (Sharp 1956; Wardle 1984; Burrow's 1996a). The arrival of the first Polynesian people led to the large-scale clearance of forests for their settlements. The dating of sub-fossil remains in the eastern South Island using radiocarbon dating techniques suggests that charcoal deposits from fires occurred between 500 and 1000 years ago (Molley *et al.* 1963).

The first European settlers arrived in 18th and 19th centuries. By this time half of the pre-human forest cover had been cleared by Polynesians (Wardle 1984). The Port Hills were largely covered in grassland and scrub at the time of early European settlement with only remnant patches of forest remaining. One such remnant was the Hoon Hay Valley. In the 1850's, "The whole of the Hoon Hay basin, plus the gullies behind, was filled with splendid bush totaras *(Podocarpus totara* and *Podocarpus hallii)* up to three metres in girth, white pine *(Dacrycarpus dacrydioides),* black pine *(Podocarpus spicatus)* and plenty of giant broadleaf *(Griselinia littoralis)* manuka (probably kanuka *(Kunzea ericoides))* and konini *(Fuchsia excorticata)"* Ogilvie (1978).

Europeans cleared the existing forests in the Hoon Hay Valley for timber, farming and as a source of fuel (Petrie 1963; Ogilvie 1978). A fire recorded in 1868 (which took two weeks to burn out) together with many unrecorded fires and over 100 years of farming have reduced the area to grassland and scrub (Ogilvie 1978; Williams 1983).

2.5.5. Present Vegetation

The present vegetation in the Hoon Hay Valley is a complex mosaic of different stages of succession, (Figure 2.2) from bare pasture to areas dominated by advanced successional vegetation (Dungan 1997). Three classes of vegetation presently found in the valley have been identified: i) semi-continuous indigenous forest ii) regenerating indigenous and deciduous exotic small trees over a canopy of broom

and iii) a secondary growth of indigenous bracken fern and native trees with patches of gorse, grass and broom (Meurk 1993). Common plant species in today's vegetation include totara *(Podocarpus hallii)* at the head of the valley and on steep southerly faces, mahoe *(Melicytus ramiflorus)*, ngaio *(Myoporum laetum),* mapou *(Myrsine australis),* lemonwood *(Pittosporum eugenioides),* kohuhu *(Pittosporum tenuifolium)* and kowhai *(Sophora microphylla)* in the gullies (Williams 1983). In the center of the upper basin, ribbonwood *(Plagianthus regius),* narrow-leaved lacebark *(Hoheria augustifolia),* kowhai *(Sophora microphylla)* and kanuka *(Kunzea ericoides)* are common, while bracken *(Pteridium esculentum)*, broom *(Cytisus scoparius)*, elder *(Sambucus nigra)*, gorse *(Ulex europaeus)*, native shrubs and pohue vines *(Muehlenbeckia australis)* dominate the scrub (Williams 1983).

Figure 2.2. The present patchy vegetation on the Hoon Hay Valley.

2.5.6. The broom→ elder→mahoe successional sequence

Vegetation in the Hoon Hay Valley is currently undergoing a recovery process following disturbances associated with human settlement and fires. Patterns of vegetation, successional interactions, the potential significance for conservation, land use options, seed dispersal patterns and soil seed bank studies have been investigated on the Port Hills (Williams 1983; Jayet 1986; Partridge 1989, 1992; Meurk 1993;

Burrows 1994a, b, c; Cullen 1996; Reay 1996; Dungan 1997; O'Cain 1997). Williams's (1983) study found that succession followed a sequence from broom through elder to mahoe. This sequence had broad similarities to the kanuka *(Kunzea ericoides)* to mahoe succession observed by Druce (1957) in the Taita experimental catchment, New Zealand, where broom and elder had taken the role of kanuka *(Kunzea ericoides)* (Williams 1983).

Williams's (1983) findings were based on measurements of structure and canopy composition of the successional scrub. He estimated that broom lives up to 15 years, after which elder tends to take over. Elder then dominates the vegetation on the sunny faces of the Valley for approximately 15 years. He also found that elder is more frequently associated with broom than gorse. However, the time required to develop a mahoe forest from an elder thicket was difficult to estimate and he provided a rough estimation of 50 years after the establishment of broom.

Williams (1983) concluded that the broom→elder→mahoe succession fitted the facilitation model of Connell and Slatyer (1977) in which later successional species could only establish and grow once earlier species have suitably modified site conditions. For example, broom provides roosts for birds that are dispersal agents for elder. Broom fixes atmospheric nitrogen and improves conditions for species that follow. Elder provides further roosting sites and attracts more birds to its fruits, and as a result facilitates the entry of bird-dispersed seeds of native forest species, such as mahoe. Elder may also create a better seedling environment due to its being a deciduous plant.

Although the succession from broom through elder to mahoe was also identified and later supported by Dungan (1997), no study has determined the mechanisms and processes which control the successional dynamics.

2.6. Hypotheses

Three hypotheses were formed on the basis that the differences in seed characteristics, light and nutrients requirements and water relations would play a vital role in successional dynamics. Each hypothesis is divided in to a sub set of hypotheses according to the experiments conducted.

Hypothesis 1

That the order of species in the broom→elder→mahoe succession is dependent on seed characteristics.

— Seed size should increase from broom<elder<mahoe.
— Seed food reserve should increase from broom<elder<mahoe.
— Seed longevity should decrease from broom>elder>mahoe.
— Light requirements for germination should increase from broom>elder>mahoe.
— Dormancy breaking requirements are related to the successional positions of broom, elder and mahoe.
— Seedling's ability to emerge from deeper soil levels should decrease from broom>elder>mahoe.

Hypothesis 2

That the order of species in the broom→elder→mahoe succession is dependent on the differences in light and nutrient requirements of each species.

— Seedling tolerance of shade should increase from broom<elder <mahoe.
— Seedling nutrient requirement should decrease from broom>elder>mahoe.
— Allocation to shoots in the shade should decrease from broom>elder>mahoe.

Hypothesis 3

That the order of species in the broom→elder→mahoe succession is dependent on the differences in water relations of each species.

— Seedling water stress tolerance should decrease from broom>elder>mahoe.
— Seedling relative water content under water stress conditions should increase from broom<elder<mahoe.
— Seedling root penetration under water stress conditions should decrease from broom>elder>mahoe.
— Seed germination under water stress conditions should decrease from broom>elder>mahoe.
— Seedling water use efficiency should decrease from broom>elder>mahoe.

Chapter 3

The plant species

3.1 Introduction

This chapter provides general descriptions of the morphology and distribution of broom, elder and mahoe and observations of their ecology in the Hoon Hay Valley.

3.2. Broom *(Cytisus scoparius)*

Broom is a fast growing leguminous shrub, 2-4 m tall, with green switch-like stems longitudinally rigid and angled. The leaves are narrow and simple but sometimes are found with 2-3 leaflets, are often absent. Broom flowers are conspicuous and bright yellow (Webb *et al.* 1988) (Figure 3.1). In New Zealand broom flowers predominantly between September to April; fruiting occurs between December and April (Webb *et al.* 1988). However, flowering broom bushes can be seen in the Valley all year round (personal observation). Mature pods (fruit) are black, oblong, between 1.5 and 6 cm long with hairy margins (Webb *et al.* 1988, Wilson and Galloway 1993). Pods may contain up to 24 seeds, although on average hold approximately 14 seeds. Seeds are brown or greenish brown, dispersed by explosive pod dehiscence in warm weather (Webb *et al.* 1988). Ants and feral mammals facilitate the longer distance dispersal of broom seeds (Smith and Harlen 1991).

Broom is native to Europe, Asia and Russia and has a life-span of approximately 10-15 years (Waloff 1968). It is an introduced species in New Zealand and abundantly distributed throughout the country. Broom is often found in sites disturbed by human activity and forms a dense successional scrub (Wilson 1994; Wilson and Galloway 1993). Although broom is considered a serious weed in farmland, its usefulness in forest restoration has also been recognized (Wilson and Galloway 1993).

Figure 3.1. Flowering broom *(Cytisus scoparius)* shrubs in the Hoon Hay Valley.

3.3. Elder *(Sambucus nigra)*

Elder (Figure 3.2) is a fast growing deciduous shrub or small tree, which grows up to 10 m with straight erect shoots originating from the base. Between November and December, large flat-topped clusters of flowers are evident. Fruiting occurs between February and March. The edible fruits are dispersed by frugivorous birds and large

clusters of drupes are characteristic in late summer and early autumn (Webb *et al.* 1988, Poole and Adams 1990). Ripe berries are black and approximately 6 mm in diameter. Each berry can contain up to 12 seeds with an average of 7 seeds per fruit.

Elder is native to Europe and scattered over all temperate regions. Elder is frequently found on waste places, road sides, scrubs, forest margins, near human disturbance activity and most other modified plant communities (Webb *et al.* 1988, Wilson 1994).

Figure 3.2. Elder *(Sambucus nigra)* bush from the Hoon Hay Valley

3.4. Mahoe *(Melicytus ramiflorus)*

Mahoe (Figure 3.3) is an evergreen, small tree up to 10 m tall, often with multiple stems with whitish wood and spreading branches. It is widespread as a canopy or sub-canopy component in lowland to lower montane mixed angiosperm-podocarp forest and has

bright yellow-green foliage (Salmon 1986). Mahoe flowers appear in dense clusters often on bare old stems from November to February and fruiting occurs between November and March (Webb *et al.* 1990; Dawson and Lucas 1993). Fruit is a small berry with a diameter of approximately 5 mm. Ripe fruits are violet-blue colour and contain up to 10 seeds. The fruits are eaten and dispersed by birds.

Mahoe is a native species abundantly found in New Zealand's North Island, South Island and Stewart Island ascending to 1000 m as a small tree in forests, gullies and coastal slopes (Salmon 1986; Webb *et al.* 1990).

Figure 3.3. Mahoe *(Melicytus ramiflorus)* tree from the Hoon Hay Valley

Chapter 4

The seed characteristics of broom, elder and mahoe

4.1. Introduction

Chapter 4 addresses the first hypothesis in order to assess the contribution from seed characteristics towards the successional pathway. The chapter begins with a background which discusses seed characteristics in relation to plant succession. Each of the experiments that follow are described separately with individual methods, results and discussion sections. A general conclusion evaluates the contribution of seed characteristics to the successional pathway broom→ elder→ mahoe.

4.1.1. The study of seeds in relation to plant succession

4.1.1.1. What is a seed?

A seed is the product of the fertilized ovule, which is characteristic of both gymnosperms and angiosperms. Gymnosperm seeds are formed 'naked', and angiosperm seeds are formed in an ovary. The seed contains the embryo, which has the potential to grow and develop into an adult plant.

4.1.1.2. The role of seeds

Generally, seed production performs four main tasks: i) the re-sorting of genetic material, ii) dispersal, iii) multiplication and iv) a survival mechanism (Bradbeer

1988). In most species seeds contain new genetic combinations as a result of segregation and recombination of genes in sexual reproduction. The seed not only enables gene dispersal away from the parent plant, but is also a facility to multiply the size of the population. One of the most important of all the seed's characteristics is its ability to lie dormant in adverse conditions until environment conditions become favourable.

4.1.1.3. Seed characteristics and vegetation succession

The change in species composition during vegetation succession has been extensively studied. Seed characteristics have been stressed as an important species attribute in succession (e.g. Fenner 1985, 1987; Fagerstrom 1989; Olff *et al.* 1994).

Plant species may enter the process of succession as seeds, at any time. However, their successful germination and establishment depends upon the site characteristics and the vegetation already present in the site. Only seeds of species which have characteristics suited to existing environmental conditions can establish successfully. In a vegetation succession, where the species composition and site characteristics are dynamic, seed properties of successful species are likely to be different according to successional status. Seed characteristics are therefore likely to be a key determinant of the order of plant establishment during succession.

The process of regeneration can be an obstacle race posed by environmental stress, competition, predation and disease that come in different nature and extent. While some species face these obstacles at early stages of the process (e.g. pollination, ripening) other species can face them later (e.g. competition during seedling establishment). In a comprehensive review of the mechanisms involved in regeneration, Grubb (1977) suggests several key points: (i) successful invasion of a gap by a plant species depends on plant processes and the characteristics of the gap; (ii) the size and shape of the gap, time of formation, orientation, nature and soil surface, presence of litter, animals and other plants, fungi, bacteria and viruses; (iii) seed production, dispersal, germination, establishment and onward growth as

important plant processes for gap invasion. Each species exhibits its own distinctive reproductive strategy, including the allocation of a given fraction of resources to reproduction, striking a balance between sexual and vegetative reproduction, fruiting at the appropriate time and producing the optimum number of seeds of an optimum size.

The sequence of floristic change which constitutes succession may be explained by an examination of the seed characteristics of the plant species which are dominant at different stages of a successional process (Fenner 1987). Regeneration from seed is dependent on the seeds being in the right physiological state at the right place at the right time (Murdoch and Ellis 1992). The regeneration process involves several stages including seed release, dispersal, dormancy, germination and seedling establishment. The obstacles to overcome within each stage include competition, predation, disease, and environmental stress. The nature and extent of these obstacles are different at each phase according to the environmental conditions at the site, the present vegetation and successional stage of the present vegetation. Seeds have a variety of mechanisms to overcome the potential difficulties encountered during the regenerative process.

Pioneer species arrive early at a newly created site largely due to having an effective means of seed dispersal (e.g. wind dispersal) of their frequent, massive seed production early in life (Tagawa *et al.* 1985; Fenner 1987; Del Moral and Wood 1988; Dale 1989; Halpern *et al.* 1990). Viereck (1966) reported the dispersal by pod dehiscence in pioneer legumes was also well suited for the environmental conditions in the site.

Nakashizuka *et al.* (1993) stressed the importance of seed dispersal to vegetation development following a volcanic eruption. Their study did not identify a strictly primary succession, rather they found a mixture of two processes. In areas that were largely devastated, primary succession developed from wind dispersal seeds, while in other areas where surface soil remained, secondary succession occurred from buried seeds and rhizomes. Del Moral *et al.* (1995) challenge the conventional views of sucession in a study of early primary succession on Mount St. Helens, U.S.A. They

claim that early primary succession is controlled by stochastic events and low probability dispersal. Season of eruption and the persistence of relict vegetation also played role in early reassembly of plant communities on Mount St. Helens while environmental factors had a limited role in governing community structure.

The life histories of plants depend on the dispersal and germination of seeds (Colinvaux 1986). Possession of a large seed is advantageous, ensuring successful seedling establishment following dispersal, because large seeds have large food reserves that can be used in the most critical period of seedling establishment. Such reserves help seedlings to be independent of external resources and allows them to develop to a stage where they are strong enough to compete with other individuals for resources. Large seeds, which store more carbon than small seeds, are compensated through a reduction in carbon assimilation in the early stages of life (Fenner 1983, Westoby *et al* 1996).

Seed size is important for successful dispersal. Seed size appears to increase in a succession (Werner & Platt 1976; Fenner 1987). Generally, colonising species have small seeds that can easily be dispersed by the wind. Plants found in closed vegetation tend to have larger seeds than those from open sites (Fenner 1985). Salisbury (1942) categorised the British flora according to seed size and found it to be correlated with habitat and successional status. His study revealed that the most frequent seed weight category for open habitat species was 0.24-0.98 mg; for mid successional species, the weight was 16 times larger than open habitat species; for later successional trees, the weight was 256 times larger than open habitat species. Leishman and Westoby (1994) suggested large seeds confer advantages in habitats where canopy gaps are regularly created, because large energy reserves enable seedlings to tolerate shade for longer periods. Seedlings from large seeds have increased height compared to smaller seeds which can be advantageous in sites with a steep gradient of light (Leishman and Westoby 1994).

Soil seed banks are also an important means of colonization (Fenner 1987). This mechanism is not available to the pioneers of a primary succession. Soil seed banks are a highly dynamic and important entity in a secondary succession (Harper 1977)

and studies from many plant communities have shown the importance of the soil seed bank to ecosystem development following disturbance (e.g. Keddy *et al.* 1989). In general, early successional species tend to maintain persistent soil seed bank and the importance of the soil seed bank tends to decrease with successional maturity (Fenner 1987). Species represented in a soil seed bank may yield information on the vegetation history of a site or convey insight into its future composition (Ray 1993). The dynamics of the seed bank may provide clues to the process of recovery of the vegetation of disturbed sites. The role of the seed bank may be more important in areas with a strongly seasonal climate than in areas where seedling recruitment is not limited to one season (Jimenez and Armesto 1992). However, most studies indicate that soil seed banks contain species with dormancy mechanisms broken by exposure and that these species tend to be light demanding pioneer species in both temperate and tropical regions (Hall and Swaine 1980; Brown and Costerhuis 1981; Cheke *et al.* 1979). Bakker *et al.* (1996) found that the larger the seed weight, the shorter the persistence in the seed bank. Thompson (1993) also observed that persistent seeds tend to have smaller, more compact seeds, while transient seeds are often larger.

The presence of a soil seed bank is not, in itself, sufficient for successful establishment. Pioneer species in secondary successions are known to have gap detecting mechanisms such as a requirement for fluctuating temperatures, or sensitivity to red:far red ratios in order to break dormancy (Thompson and Grime 1983). An analysis of the germination of 91 herbaceous species in response to a temperature gradient, alternating temperatures and stratification during grassland succession, demonstrated that changes in species composition at different stages in succession were related to changes in germination attributes during the succession towards nutrient poor grassland (Olff *et al.* 1994). The germination requirements of each plant highlights the adaptive ability of a plant. Plants exhibit different germination requirements which are adaptive in terms of the possible hazards which may be faced as there is no certainty that the seed will fall onto a suitable substrate to start life. Dormancy safeguards the seed from commencing germination when a site is unsuitable.

During the later stages of secondary succession, a soil seed bank becomes irrelevant, as the seeds of later successional species are generally short-lived. A study which investigated soil seed banks in the dry Afro-montane forests of Ethiopia showed that while the herbs had the largest number of seeds in the seed bank, the contribution of tree species to the bank was generally low (Teketay and Anders 1995). For example, in Britain, there exist relatively high similarities between vegetation and seed banks in annual dominated vegetation, but comparatively low similarities in most perennial salt marsh communities (Ungar and Woodell 1993). Milton (1939) also found that dominant perennials were under-represented in the seed banks. Therefore later successional species often maintain a population of seedlings under canopy (Fenner 1987). When these seedlings are released from shade they grow quickly (Canham 1985) ensuring a rapid response to canopy gaps. Seed attributes and germination characteristics obviously play an important role in determining the species occurrence sequence in a succession.

4.2. Materials and Methods

4.2.1. Seed collection and storage

Seeds of elder, broom and mahoe were collected from the Hoon Hay Valley, according to their availability, on several occasions during December 1995-February 1996, October-December 1996 and February-March 1997. The ripe fruits of elder were collected from 5 individual trees at each time on four occasions. Fruits were gently macerated and fruit coats were washed away through a sieve. Extracted seeds were dried for two weeks at room temperature and mixed together. Seeds were then either used in experiments as fresh seeds or stored until further use in sealed polythene bags in a refrigerator or at room temperature. Ripe fruits of mahoe were collected from 10 individual trees on two occasions. Mahoe seeds were extracted and air-dried as for elder. Mature pods of broom were collected from 20 bushes on two occasions. Pods were air-dried and seeds were collected after the pods opened. In order to reduce seed loss, pod trays were covered with thin cloth. Seeds were stored as described above.

4.2.2. Experiments

Seed weight attributes were examined in terms of the relationships between seed weight, embryo weight, seedling weight and embryo fraction. Viability was examined in fresh seeds and stored seeds. Seed germination requirements were investigated in terms of their response to scarification, temperature stratification, and light. The effects of soil depths on seedling emergence were also examined. Detailed methods are described below.

4.2.3. Data analysis

Microsoft Excel 97 SR-2 and SAS/STATS 6.12 (1995) were used for statistical analysis. Analysis of variance procedures, GLM procedures for unbalanced data, analysis of correlation were performed depending on the experiment. When significant differences were observed between means, further tests were carried out to determine the strength of the differences. Although Duncan's test is widely used it was decided to use Tukey's test because it gives confidence intervals, works with unequal cell sizes and is a more robust test for non-normality of data (Zar 1984, Williams 1993). Furthermore, Duncan's test was proposed for interpretation of a set of treatments that have no structure or pattern unlike the structured nature of the present experiments. When percentages were involved in the analysis they were arscine transformed as this results in an underlying distribution that is nearly normal (Zar 1984).

4.3. Seed weight attributes

4.3.1. Determination of seed weight

Thirty-five batches of seeds, each containing 100 well-developed seeds from each species were weighed and the mean seed weight was calculated.

4.3.2. Determination of food reserves

An ample amount of hydrated and appropriately pre-treated seeds were sown on filter paper moistened with distilled water in petri-dishes in order to select a sample (40 from each species) for the experiment. Pre-treatments were used to obtain as uniform germination as possible. For all species, soaking water was changed 12 hourly during hydration in order to wash away any germination inhibitors. Scarification was not performed because it would affect the weight of the seed coat. Elder seeds were subjected to temperature stratification ($20^0C/4^0C$) as described in section 4.6 as a pre treatment. Upon germination, forty seedlings from each species were transplanted carefully into perlite in individually divided planting trays, each contained 20 cm^3 perlite. Seedlings were watered with distilled water in alternate days and no fertilizers were added. This experiment was carried out under glass-house conditions ($20^0C/16^0C$ temperature and 16 hour light). Planting trays were covered with polythene in order to reduce evaporation. Each seedling was marked with the planting date in order to obtain the correct seedling age because of slight differences in the start of germination. Seedlings were harvested at 4 weeks after planting and dry weights determined. Embryo weight (embryo +endosperm) was determined by subtracting the weight of air-dried seed coats shed by germinating seeds from their initial seed weights recorded before soaking in water. Percentage contribution to the seed weight by the embryo (embryo +endosperm) was then determined to give the embryo fraction. Mean seed weight, embryo weight (embryo +endosperm), seedling weight at 4 weeks and embryo fraction (embryo +endosperm) were compared between species and correlations between variables were tested.

4.3.3. Results

4.3.3.1. Seed weight

Mean seed weight decreased in the order of broom>elder>mahoe. The mean seed weight of broom, elder and mahoe was 0.0099, 0.0023 and 0.0012g respectively. One-way ANOVA procedure in SAS showed a highly significant difference in seed weights between species ($F(2,102)=597.7$, $P\leq0.001$) and Tukey's test revealed a significant difference between the means of the three species (Table 4.1).

Table 4.1. Mean seed weights of broom, elder and mahoe. (Means indicated by the same letter are not significantly different (Tukey's test, $P\leq0.05$)).

Species	N	Grand mean (g)	Std Dev. (g)	Minimum (g)	Maximum (g)
Broom	35	0.0099 a	0.0019	0.0055	0.0144
Elder	35	0.0023 b	0.0006	0.0007	0.0035
Mahoe	35	0.0012 c	0.0003	0.0007	0.0022

4.3.3.2. Food reserves

A corresponding increase in both embryo and seedling weight was found as seed weight increased in the order mahoe<elder<broom (Table 4.2). However, the percentage contribution made by the embryo to the total seed weight was not significantly different between species.

One-way ANOVA procedures indicated significant differences ($P\leq0.001$) in seed weight ($F(2,117)= 674.6$), embryo weight ($F(2,117)= 365.6$, and seedling weight ($F(2,117)=85.5$) while differences in the embryo fraction was not significant. Pairwise comparisons of means revealed seed weight was significantly different

between all three species. However, embryo weight and seedling weight of elder and mahoe were not significantly different. (Table 4.2).

Table 4.2. Seed weight, embryo weight, embryo fraction and seedling weight at 4 weeks of broom, elder and mahoe. (Means with the same letter are not significantly different ($P \leq 0.05$)).

Species	Seed weight (g)	Embryo weight (g)	Embryo fraction	Seedling weight at 4 weeks (g)
Broom	0.0095 a	0.0061 a	60.932 a	0.0173 a
Elder	0.0023 b	0.0014 b	60.799 a	0.0074 b
Mahoe	0.0012 c	0.0009 b	62.019 a	0.0057 b

A correlation analysis was performed between variables for each species. The results are summarized in Table 4.3. There were highly significant positive correlations between all variables for broom. For elder, there was no significant correlation between embryo fraction & seed weight and embryo fraction & seedling weight, while all other variables were significantly correlated. For mahoe, there was no significant correlation between embryo fraction and seedling weight while all other variables were significantly correlated. Figure 4.1 shows the relationships between mean seed weight, embryo weight, seedling weight at 4 weeks and embryo fraction of the species.

Table 4.3. Correlation analysis of embryo weight (ew), seed weight (sw), seedling weight (sdlw), embryo fraction (ef). (* = correlation between variables is significant at P≤0.05; ** = correlation between variables is significant at P≤0.01; *** = correlation between variables is significant at P≤0.001).

Species	Variable comparison	Corre. Coefficient	Significance
Broom	Ew & sw	0.965	***
	Sdlw & sw	0.693	***
	Ef & sw	0.700	***
	Sdlw & ew	0.676	***
	Ef & ew	0.859	***
	Ef & sdlw	0.538	***
Elder	Ew & sw	0.963	***
	Sdlw & sw	0.810	***
	Ef & sw	0.176	not sig.
	Sdlw & ew	0.752	***
	Ef & ew	0.427	**
	Ef & sdlw	0.060	not sig.
Mahoe	Ew & sw	0.983	***
	Sdlw & sw	0.677	***
	Ef & sw	0.314	*
	Sdlw & ew	0.675	***
	Ef & ew	0.477	***
	Ef & sdlw	0.226	not sig.

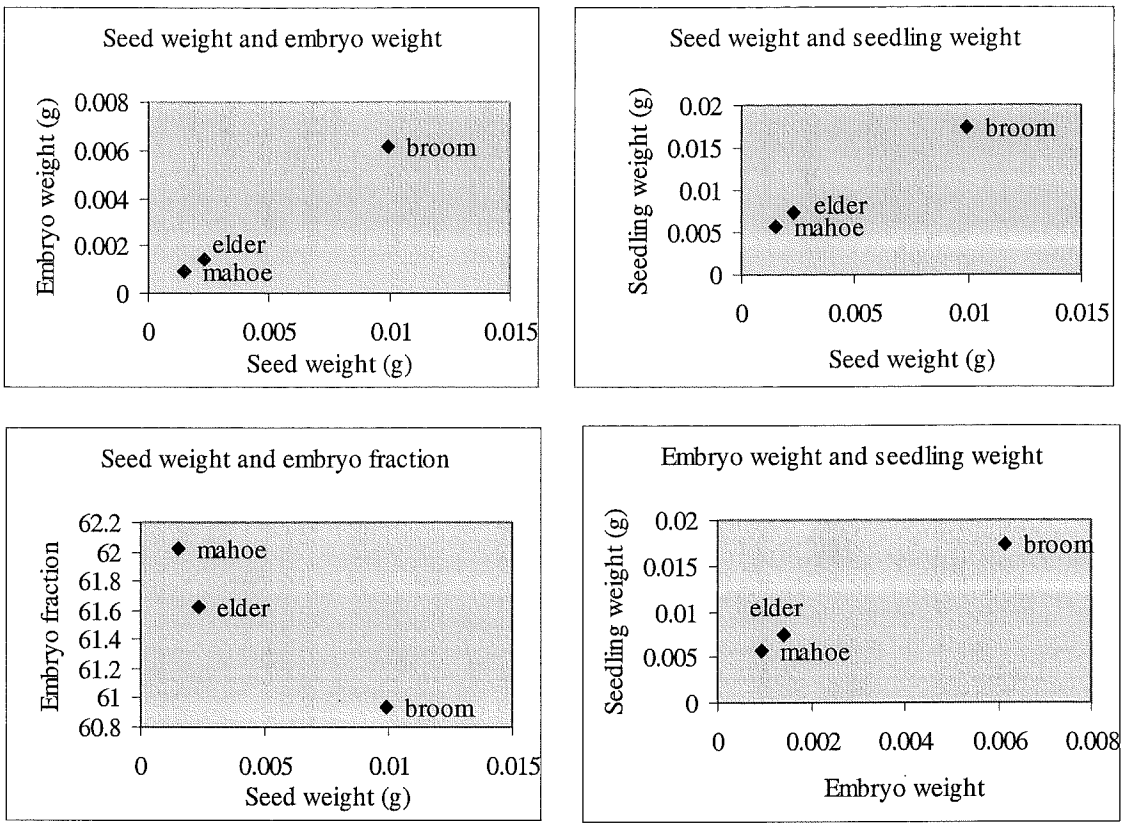


Figure 4.1. Relationship between seed weight, embryo weight, seedling weight and embryo fraction of broom, elder and mahoe.

4.3.4. Discussion

Seed size generally increases with advancing succession (e.g. Fenner 1987; Primark 1979; Werner and Platt 1976). Assuming seed weight is a rough approximation of the supply of potential energy for the seedling, a generalised relationship between seed size and successional status suggests the larger seeds are related to a more advanced phase of succession, (Salisbury 1942). Primark (1979) also showed seeds from closed habitat species are generally larger than those from open habitats. According to the above generalizations, seed weight could be expected to increase through the postulated successional sequence of broom through elder to mahoe. These results do not support that generalization as seed weight decreased from broom (0.010 gm), through elder (0.002 gm) to mahoe (0.001 gm).

However, provided they are successfully dispersed, the heavier seeds of broom may be favoured for establishment in harsher, open sites because a readily available food supply enables establishment at this crucial time. Although broom faces a dispersal disadvantage because of a relatively heavy seed, the efficient ballistic seed dispersal method overcomes the weight limitation. This dispersal method is efficient only over a few metres and not as effective as fleshy fruits. In fact, this method is more suitable for invading exposed sites or grassland where there are few frugivorous birds.

The seed size of elder and mahoe is less important to their dispersal as their main dispersal agents are frugivorus birds. If elder and mahoe follow broom in the successional sequence, according to seed size generalizations, we should expect larger seeds for elder and mahoe. However, seed size was found to decrease with the advancing succession.

According to Fenner (1983), seed weight increases with successional maturity, as a larger food reserve conveys to the seedling a competitive advantage under the low light conditions typical of mid and late successional stages. Gross (1984) also proved that seedlings from large seeds are better able to face competition from surrounding plants. Seedlings from large seeds have a height advantage over small-seeded species by having a stronger etiolation response to shade (Leishman and Westoby 1994). However, mahoe seeds were found to be the smallest among the three species tested, yet mahoe was suggested by Williams (1983) as the most advanced plant in the postulated successional pathway. This finding is supported by Augspurger (1984), who noted that survival in the shade was not so much correlated with seed weight as it was with the successional status of the species. In addition, Fenner (1978) also reported no correlation between seed size and a seedling's ability to establish in gaps in turf. The seed size of a given plant species represents a compromise between the requirement for dispersal and establishment (Harper 1977).

The relationship between seed size and seedling growth was assessed in an experiment investigating food reserves and embryo size. With increasing seed weight (from mahoe through elder to broom) both embryo and seedling weight significantly increased. Statistically significant differences in the embryo fraction (the percentage

contribution made by the embryo to the total seed weight) were not found between the three species, although there was a trend towards an increase in the embryo contribution to the seed weight in the order of broom (60.9%) > elder (61.6%) > mahoe (62%).

The results documented here do not support the generalizations about seed weight changes in successions (e.g. Fenner 1983; Salisbury 1942; Primark 1979). This may be because all three species belong to early successional stages. Seed weight, on its own, may therefore not always be taken as sensitive indication of a plant's successional phase.

4.4. Seed viability over time

4.4.1. Methods

The viability of fresh and stored seeds was tested using tetrazolium staining (TTC) (Mackey 1972; Moore 1972). Both fresh and stored seeds were used for this experiment. Stored seeds included three storage times; 6, 12 and 24 months at two temperatures; room temperature (approximately 20^0 C) and refrigerator (approximately 5^0 C). Seeds from each species were surface sterilized in 1% sodium hypochloride for 15 minutes, then soaked in autoclaved distilled water for 24 hours in the dark. Five replicates of 10 seeds from each species (totalling 50 seeds from each species) were then cut length-wise with a sterile razor blade and immersed in 1% aqueous triphenyltetrazolym chloride solution (TTC) for 8 hours at room temperature. Seeds were examined for embryo stain. During this experiment, extra care was taken to maintain sterile conditions because any other respiring tissue would give a positive result to TTC. Stained embryos were counted as viable and % viability was determined. Changes in seed viability was tested between species at different storage times and different storage methods.

4.4.2. Results

Broom and mahoe seeds were 100% viable when fresh. Elder seeds displayed 84% viability as fresh seeds. The viability of broom ranged between 94-100% following storage, irrespective of the storage temperature. Elder showed 80% viability after two years in storage while the seed viability of mahoe declined to 78% after two years (Table 4.4).

SAS GLM procedures showed significant differences in seed viability between species ($F(2,98)=53.3$, $P\leq0.001$), the method of storage ($F(2,98)=5.9$, $P=0.004$) and the storage time ($F(2,98)=11.2$, $P\leq0.001$). Tukey's test was carried out to test for differences between species and tested variables (Table 4.5). Seed viability was significantly different between all three species. When the method of storage was considered, the viability of broom was significantly different ($P\leq0.05$) between storage types with the exception of fresh seeds and those stored in the refrigerator (f & sf). No significant effect of any storage methods on seed viability was found for elder. Mahoe seed viability was significantly different only between fresh seeds and seeds stored in refrigerator ($P\leq0.05$).

When storage time is considered, Tukey's test showed that decrease in seed viability with increasing time was not significantly different for either broom or elder. The decrease in mahoe seed viability was significant in all comparisons except fresh seeds and seeds stored for 6 months comparison (Table 4.5).

Table 4.4. Mean percentages (± SE) of seed viability of broom, elder and mahoe.

Storage method	Storage time	Broom	Elder	Mahoe
Fresh	0	100 ± 0	84 ± 2.4	100 ± 0
Room temp. (20^0 C)	6 months	96 ± 2.4	84 ± 2.4	100 ± 0
	12 months	94 ± 2.4	84 ± 2.4	94 ± 2.4
	24 months	94 ± 2.4	80 ± 3.2	82 ± 2
Refrigerator (5^0 C)	6 months	100 ± 0	84 ± 2.4	96 ± 2.4
	12 months	98 ± 2	82 ± 3.7	90 ± 0
	24 months	98 ± 2	80 ± 4.5	78 ± 2

Table 4.5. Tukey's test for percentage seed viability. (f = fresh, sr = stored in room temperature, sf = stored in fridge. * indicates comparisons significant at P≤0.05).

Variables	Species	Comparisons	Result
Storage method (with all storage times pooled)	Broom	f - sf	n.s
		f - sr	*
		sf - sr	*
	Elder	f - sf	n.s
		f - sr	n.s
		sf - sr	n.s
	Mahoe	f - sr	n.s
		f - sf	*
		sr - sf	n.s
Storage Time (with all storage methods pooled)	Broom	0 - 6	n.s
		0 - 12	n.s
		0 - 24	n.s
		6 - 12	n.s
		6 - 24	n.s
		12 - 24	n.s
	Elder	0 - 6	n.s
		0 - 12	n.s
		0 - 24	n.s
		6 - 12	n.s
		6 - 24	n.s
		12 - 24	n.s
	Mahoe	0 - 6	n.s
		0 - 12	*
		0 - 24	*
		6 - 12	*
		6 - 24	*
		12 - 24	*

4.4.3. Discussion

The pattern of seed viability following storage for two years (either at room temperature or in refrigerator) was broom> elder> mahoe where mean percentage viability was 94%, 80% and 78% respectively. The ability to maintain a high seed viability for more than one year provides flexibility to cope with both intra- and inter-yearly fluctuations in environmental conditions. Extended seed viability suggests these species are important contributors in the soil seed bank. A seed bank is a typical characteristic of early successional species in a secondary succession (Fenner 1987).

There is evidence to suggest that broom seeds might maintain viability for a very long time (Turner 1934). The seed bank of the Port Hill soils is known to have a significant broom seed component (Partridge 1989). Broom forms a persistent deeply buried seed bank, even where the above ground vegetation does not include broom (Partridge 1989), presumably a result of previous vegetation prior to disturbance.

The successional sequence postulated by Williams (1983), suggests mahoe enters the succession at a later stage, where vegetation is approaching a secondary forest. Having a soil seed bank is not a characteristic feature of a later successional species and seeds of these species tend to be short lived and lack prolonged dormancy (Fenner 1987). That mahoe seeds remained viable in storage for two years and showed up to 78% viability indicates a possible role of the soil seed bank in the regeneration of mahoe, although viability may have been lower under field conditions, especially when considering fungal decay, which could apply for all three species. The evidence that mahoe is a species consistently present in the soil seed bank (Partridge 1989) suggests broom, elder and mahoe are all early successional species; Mahoe could be considered as a species found in the later period of early succession.

4.5. Germination response to seed scarification

4.5.1. Methods

Seeds stored at room temperature (approximately 20 ^{0}C) for 6 months were used in this experiment. Seeds were scarified by gentle rubbing on sand-paper until small chips of testa appeared on the paper. The seeds were then soaked in distilled water for 48 hours. Soaking water was changed every 12 hours.

Soaked seeds were placed in petri-dishes (20 in each petri-dish) on moistened filter paper. There were 5 replicates for each species. Well-hydrated, un-scarified seeds were used as the control. Petri-dishes were placed in a growth cabinet at 12 hr light, 60% relative humidity (r.h.) 18^{0}C and 12 hr dark, 65% r.h. 15^{0}C. Seeds were examined every third day; germinated seeds were counted and removed from the experiment. Dampened filter papers were changed weekly to minimize fungal attack. Both broom and mahoe germination was completed within two months. Elder did not germinate rapidly and it was necessary to extend the experiment further (up to 22 weeks). At the end of the experiment, the remaining seeds were tested for viability using TTC. Percentage germination was calculated and the effect of scarification on seed germination was analyzed.

4.5.2. Results

In both treatments, broom seed germination began at 3 days with 9% of the seeds germinated at the start in the scarified treatment in comparison with 1 % in the un-scarified treatment. The scarified broom seeds achieved maximum germination at 18 days while un-scarified seeds took 45 days to achieve 88% germination.

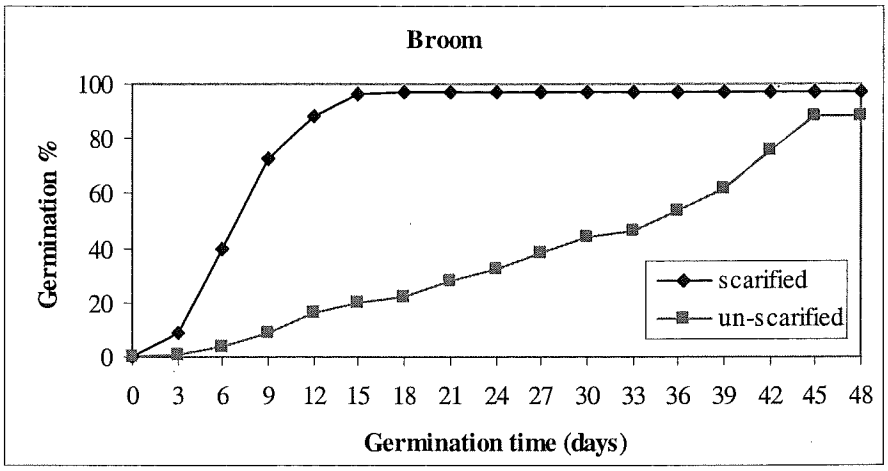
Mahoe seeds also showed an increase in seed germination when subjected to scarification. Mahoe began germination at 12 days; 15% of the seeds germinated in the scarified treatment and 2% germination in the control. Mahoe seeds in the

scarified treatment obtained a maximum of 99% germination in 33 days, as compared with 42 days to obtain 97% of germination in the un-scarified treatment. Elder seed germination was extremely low in both treatments with a maximum of 4% in the scarified treatment and 3% in the un-scarified treatment after 22 weeks.

The effects of seed scarification on the mean cumulative percent germination of broom, elder and mahoe are presented in Figure 4.2. A Two-way analysis of variance revealed significant differences in seed germination between species ($F(2,26)=22.7$, $P\leq0.001$) and treatments ($F(1,26)=68.6$, $P\leq0.001$). Further analysis was undertaken to check the effect of scarification at species level. Results showed seed scarification had a significantly different effect on the final germination of broom ($F(1,8)=119.9$, $P\leq0.001$). The differences in seed germination between scarified and un-scarified seeds of elder and mahoe were not significantly different. However, the time taken to achieve 50% final germination was significantly increased in scarified treatment compared with un-scarified treatments of not only broom but also mahoe.

TTC tests at the end of the experiment on un-germinated broom and mahoe seeds showed that all were viable except 3 rotten seeds (2 broom and 1 mahoe) in the scarified treatment. The rotten seeds appeared to have been a result of damage during scarification. There were 193 un-germinated elder seeds out of 200 used in the experiment. Viability test for these seeds revealed that 75% (145 seeds) of the seeds were viable and the rest rotten or dead due to over scarification.

a)



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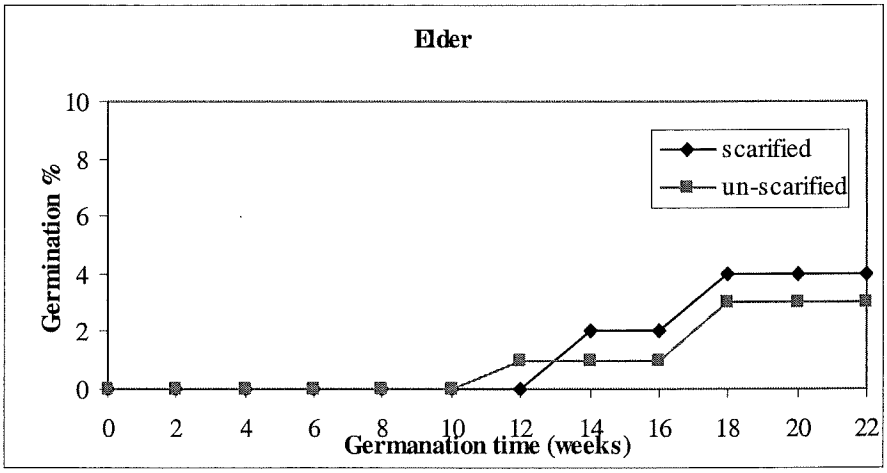

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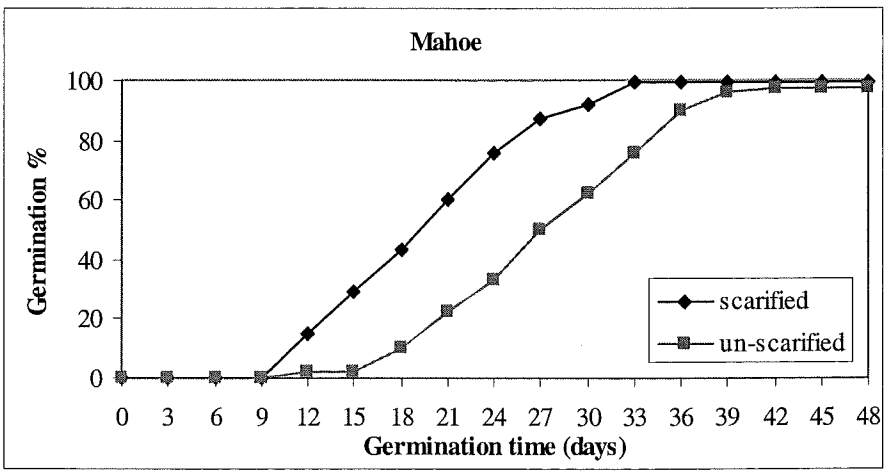


Figure 4.2. The effect of seed scarification on the germination of a) broom b) elder and c) mahoe.

4.5.3. Discussion

Seed scarification of broom by means of sand papering significantly enhanced the mean final germination over the control with germination percentages of 97% and 88% respectively after 48 days. In addition, broom seeds obtained maximum germination (97%) in 15 days while it took 45 days for un-scarified seeds to achieve maximum germination (88%). These results suggest broom may remain dormant due to an impervious seed coat. Seed coat imposed dormancy of broom has also been reported by Young and Young (1986) and Browse (1979). Smith and Harlen (1991) found scarification to induce broom up to 100% germination. Abdallah *et al.* (1989) mentioned the difficulties of germinating broom using 11 month old seeds, where only 25% of untreated seeds were able to germinate after 4 weeks. This is comparable to the present trial where, after 27 days the germination of broom in the control was 38% (Figure 4.2a). According to Bossard (1993) no more than 50% of un-scarified broom seeds germinated within 32 days in her experiments. This closely matches findings from the present investigation, although it is in contrast with the findings of Grime *et al.* (1981) in which 73% of freshly collected seed and 90% of the seed stored 6 months at 5^0C germinated after 15 days. It is apparent that higher levels of broom germination can be achieved over a longer period of time, without scarification. The ability of broom to germinate either as fresh seeds or following a dormant period indicates flexibility enabling effective seedling establishment in favourable environmental conditions, or dormancy until such conditions occur.

Scarified mahoe seeds had 99% final germination compared to 97% final germination in the un-scarified treatment, indicating the ability of mahoe to germinate, irrespective of presence of the seed coat, even though the germination rate was significantly less in the un-scarified treatment. Burrows (1995a) found 24% germination for mahoe even while still in fruit. Such flexibility in germination can be advantageous for mahoe if fruits are not ingested.

No significant effect of scarification on the germination rate of elder seeds was found, suggesting the seed coat may not responsible for its dormancy. However, the

hard seed coat of elder might have other advantages, such as permitting the seed to resist damage during passage through an avian digestive system while capitalizing on the dispersal advantages (Burrows 1995a; Williams 1983) and may even need to be passed through a vector's gut to soften the seed coat enabling germination. However, O'Cain (1997) found no germination of elder even after passing through possum guts.

4.6. Germination response to temperature stratification

4.6.1. Methods

This experiment was designed to simulate natural soil conditions experienced by seeds using growth cabinet conditions. Broom was excluded from this experiment, as that species showed high germination rates following scarification, indicating seed dormancy was due to the impermeable seed coat rather than physiological dormancy. Although mahoe seeds germinated well in the other trials it was decided to include that species because mahoe was listed in a Conservation New Zealand pamphlet as a plant with a requirement for a stratification to ensure germination (Anon. 1987).

Thirty six petri-dishes of each species, containing 20 moistened seeds in each, were subjected to two different initial warm temperatures (15^0C and 20^0C). Under each temperature, seeds were maintained for three different time periods with 6 replicates depending on the species. For mahoe, time periods in each initial temperature were chosen as 1 week, 2 weeks and 3 weeks because mahoe showed earlier germination than elder in previous experiments. For elder the time periods in the initial temperatures were 2 weeks, 4 weeks, and 8 weeks. Figure 4.2 is a diagrammatic representation of the treatments for elder. In this illustration each treatment is named according to the order of initial temperature, number of weeks in the initial temperature, temperature of the cold phase and the second warm temperature, if any, for easy reference. After the initial warm periods the petri-dishes were transferred to a cold phase (4 ^{0}C). When the germination began in any of the six replicates in each treatment half of the petri-dishes (3) were transferred to a second warm period of

15^0C or 20^0C depending on the initial temperature, while the rest of the replicates remain in the cold phase. Mahoe was not subjected to a second warm period because all replicates had reached maximum germination before the start of the second warm period. In addition to those treatments a warm only (15^0C or 20^0C) treatment was used as a control. Light level in the growth cabinet was approximately 35 mol m^{-2} day^{-1}. The temperatures were chosen to reflect natural soil conditions in late summer to early spring. Initial warm period reflects seed fall in late summer to early autumn while cold phase gives winter temperature. Second warm phase reflects early to late spring temperature.

Seeds were observed weekly for elder and at three-day intervals for mahoe and watered as required. Germinated seeds were counted and removed from the experiment. Effect on germination by initial temperature, length of time in the initial temperature and second warm period were analyzed.

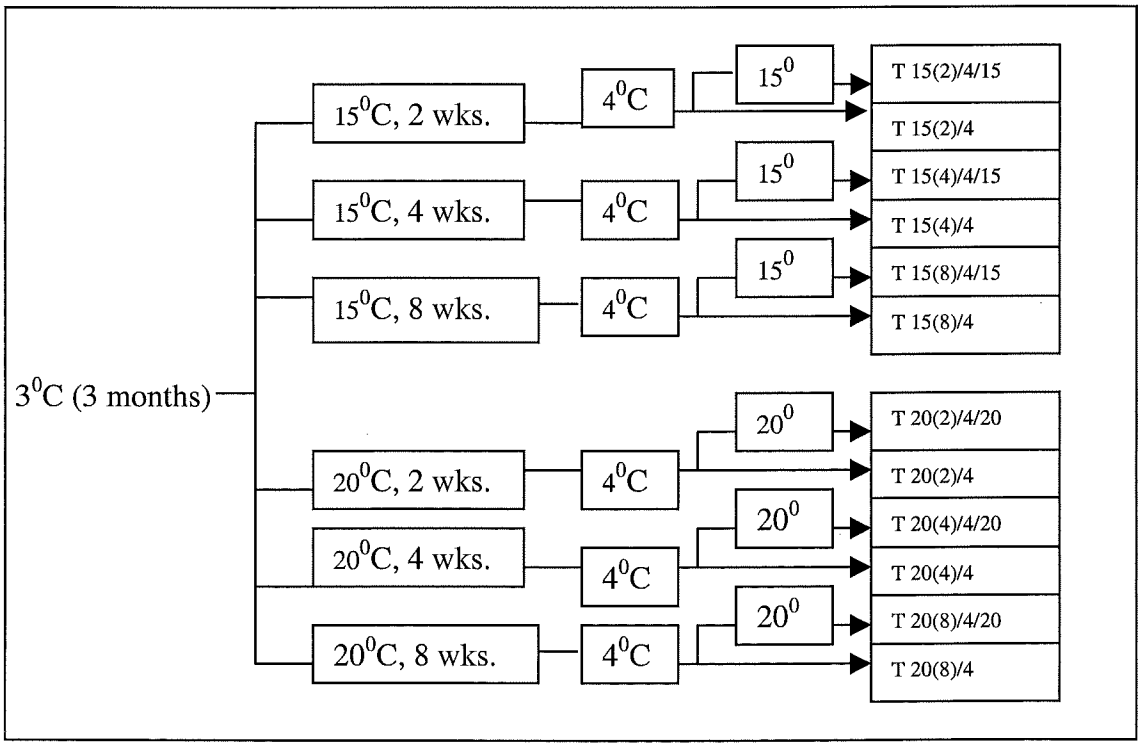


Figure 4.3. Diagrammatic representation of the treatments in the temperature stratification trial of elder.

In an additional experiment, 100 fresh elder seeds were sown in petri-dishes on moistened filter paper and were left in a house backyard for approximately one year under natural day/night and temperature conditions. Seeds were observed on a weekly basis and moistened as required. Every 4-5 weeks seeds were washed with 1% Sodium hypocloride in order to prevent fungal attack. Germinated seeds were counted and removed from the experiment.

4.6.2. Results

After having an initial warm period (15^0C) of 2,4, and 8 weeks, germination of elder started at 16, 17 and 15 weeks respectively in the cold phase of the experiment with the germination percentage ranging from 2.5-8.3%. Maximum germination achieved by elder at 15^0C initial temperature was 31.6% in the 8 weeks initial warm period treatment.

When the temperature of the initial warm period increased to 20^0C, germination started after 14 weeks into the cold phase for both 4 week and 8 weeks of initial temperature treatments while in the 2 weeks of warm period treatment, germination started after 15 weeks into the cold phase. The germination percentage at the start ranged from 4.16-5.83%. The maximum percentage achieved by elder at the end of the experiment was 60% in the 8 weeks of warm period at 20^0C and 4^0C thereafter treatment (T 20(8)/4). 55% germination was achieved in 20^0C for 8 weeks and 4^0C thereafter and then a second warm period of 20^0C treatment. (Figures. 4.4 a, b)

The introduction of a second warm period did not increase germination; in fact germination showed a decrease at both 15 and 20^0C temperature levels.

SAS GLM procedures examined the influences of initial temperature, duration of the initial temperature and the second warm period on germination. Significant differences in the germination of elder were found between different time periods, initial temperature and second warm phase. Analysis of the influence of initial temperature, period and second warm phase revealed the increase in germination in

$20C^0$ initial temperature was significantly different compared with the $15C^0$ initial temperature. The period between 2 weeks and 4 weeks in the initial temperature did not have a significant influence on germination while there were significant differences in 4 weeks and 8 weeks of warm period and 2 the weeks and 8 weeks of warm period. Where a second warm period was used as a treatment, there was no significant difference between 20C-$4C^0$ and $20C^0$-$4C^0$-$20C^0$ treatment and $15C^0$-$4C^0$ and $15C^0$-$4C^0$-$15C^0$ treatment.

Germination started in the control dishes after 17-19 weeks with a mean maximum of 3.3 % germination. Elder seeds, left under natural conditions in petri-dishes showed first germination after 26 weeks into the trial with 3 seeds germinating and germination continued at a rate of several seeds per month until the termination of the experiment, after almost a year, with a total of 38 seeds (38%) germinated.

Germination of mahoe seed began after 1-2 weeks in all treatments at both temperature levels. The mean percentage germination at the beginning was greatest in the 20^0C initial temperature level, ranging from 7.5-19.16%. At the 15^0C initial temperature level, the mean germination at the beginning ranged from 3.3- 10%. Mahoe reached maximum germination at 6-7 weeks in the $15^0C/4^0C$ temperature level while at $20^0C/4^0C$ temperature the maximum percentage was achieved in 4-7 weeks and the maximum germination was over 95% in every treatment (Figures 4.5 a, b). When considering the period spent in the warm treatment a significant difference was found between the 1 & 3 weeks comparison. Although seed germination of mahoe was increased when the warm phase temperature increased, no statistically significant influence of the initial temperature was found for the germination of mahoe seeds.

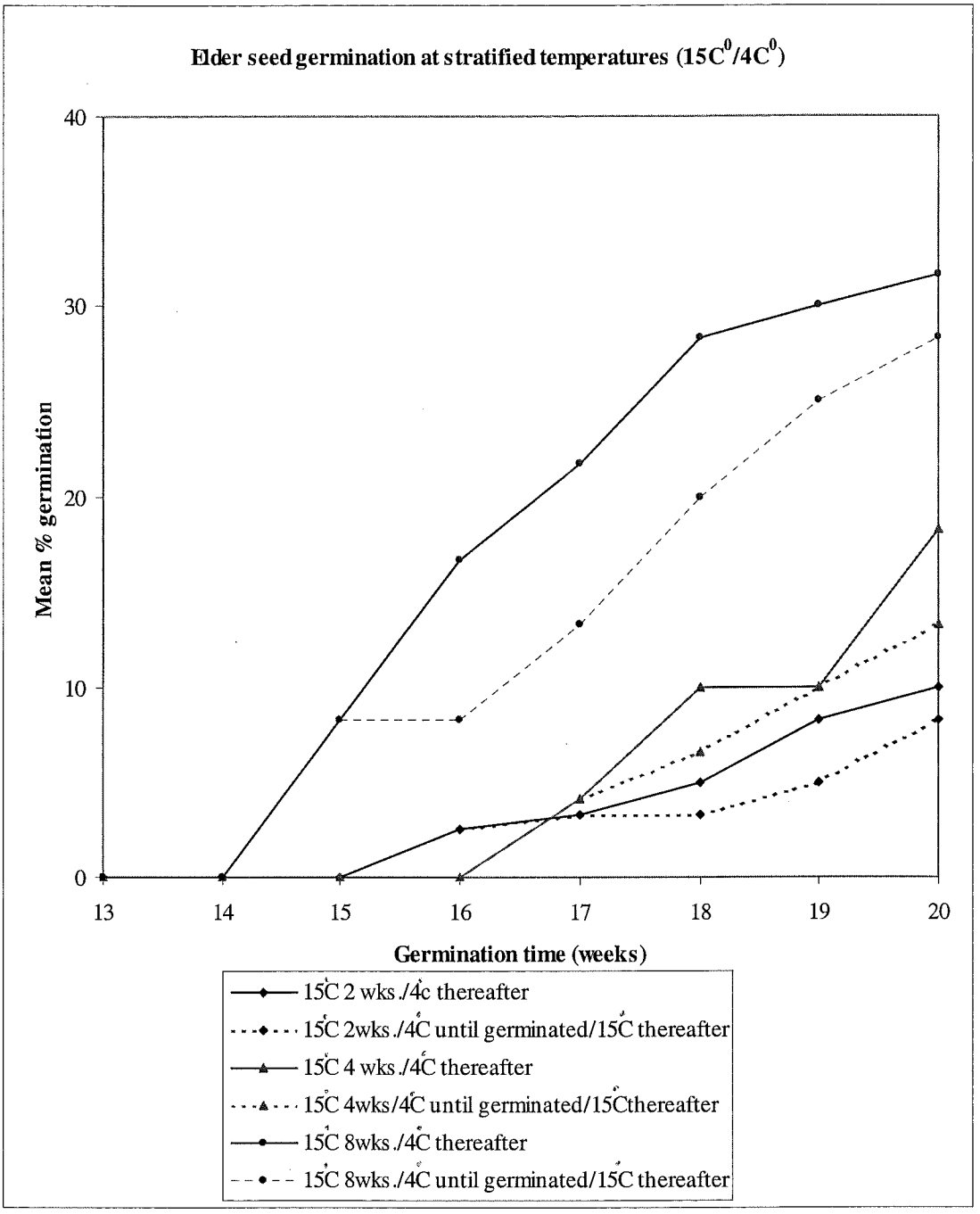


Figure 4.4 (a): Elder seed germination at stratified temperatures: $15^0C/4^0C$ temperature- initial warm period of 2, 4, 8 weeks. Additional line indicates second warm period after the germination had been started.

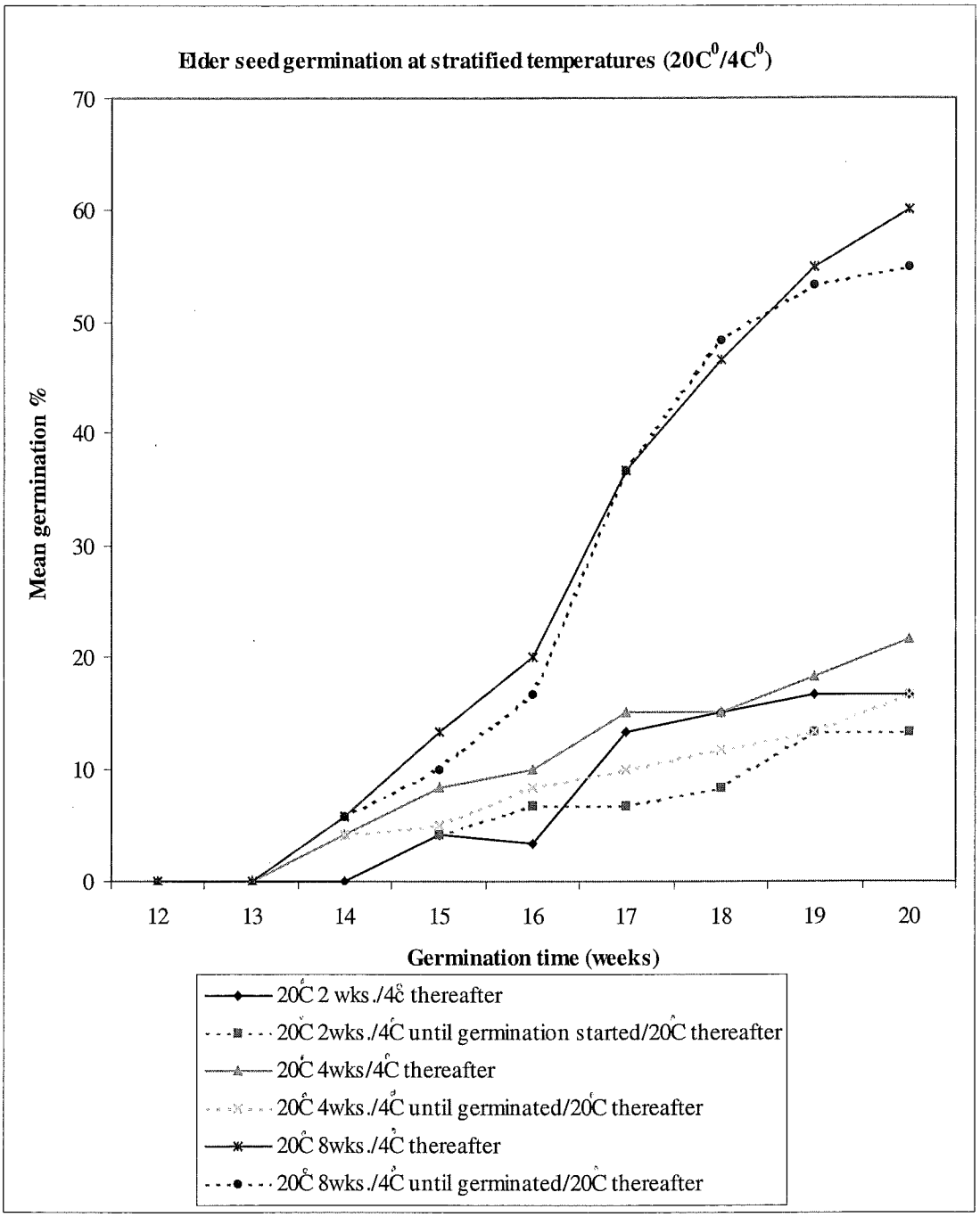


Figure 4.4 (b): Elder seed germination at stratified temperatures: $20^0C/4^0C$ temperature- initial warm period of 2, 4, 8 weeks. Additional line indicates second warm period after the germination had been started.

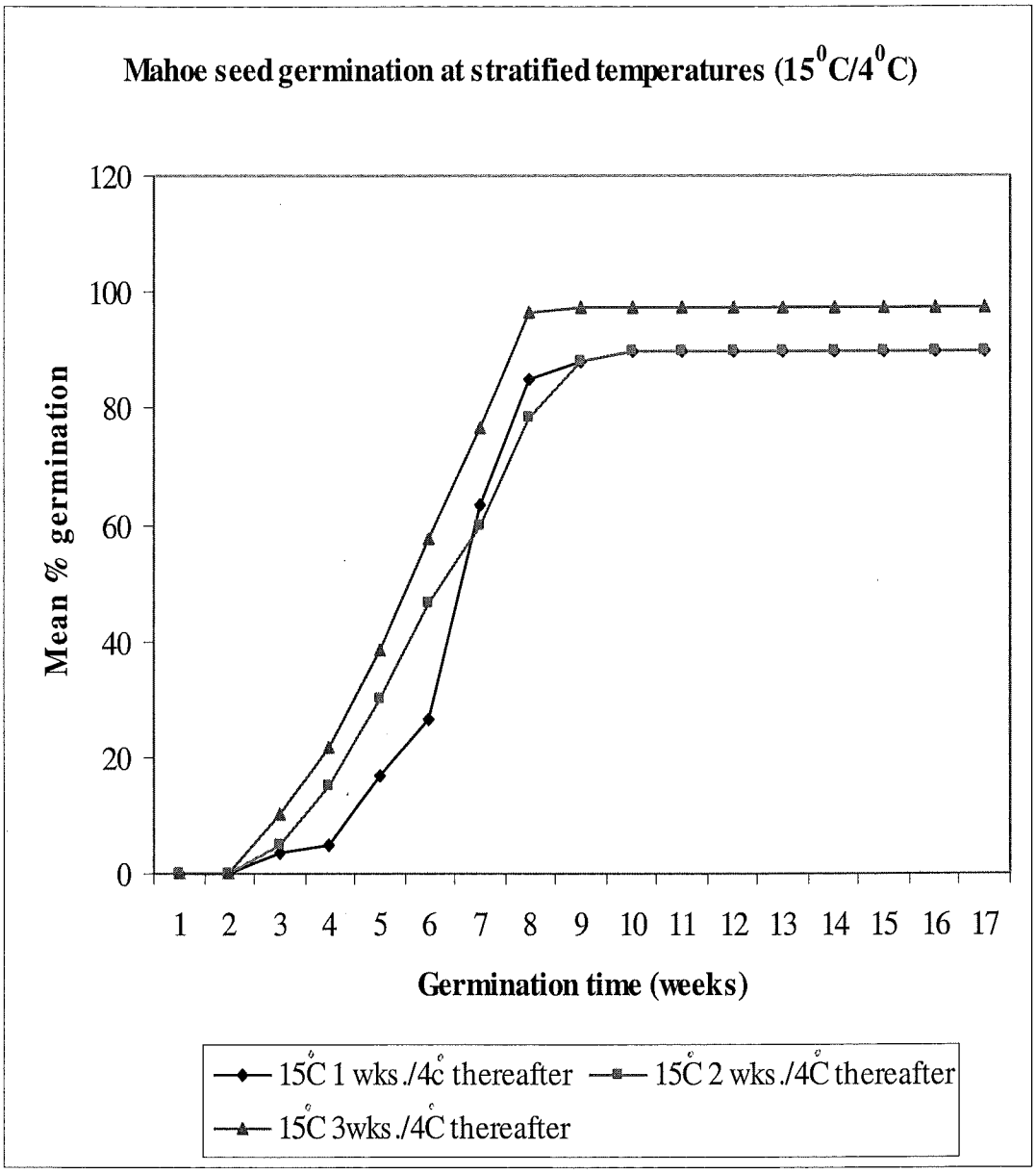


Figure 4.5 (a). Mahoe seed germination at stratified temperatures: $15^0C/4^0C$ temperature- initial warm period of 1, 2, 3 weeks.

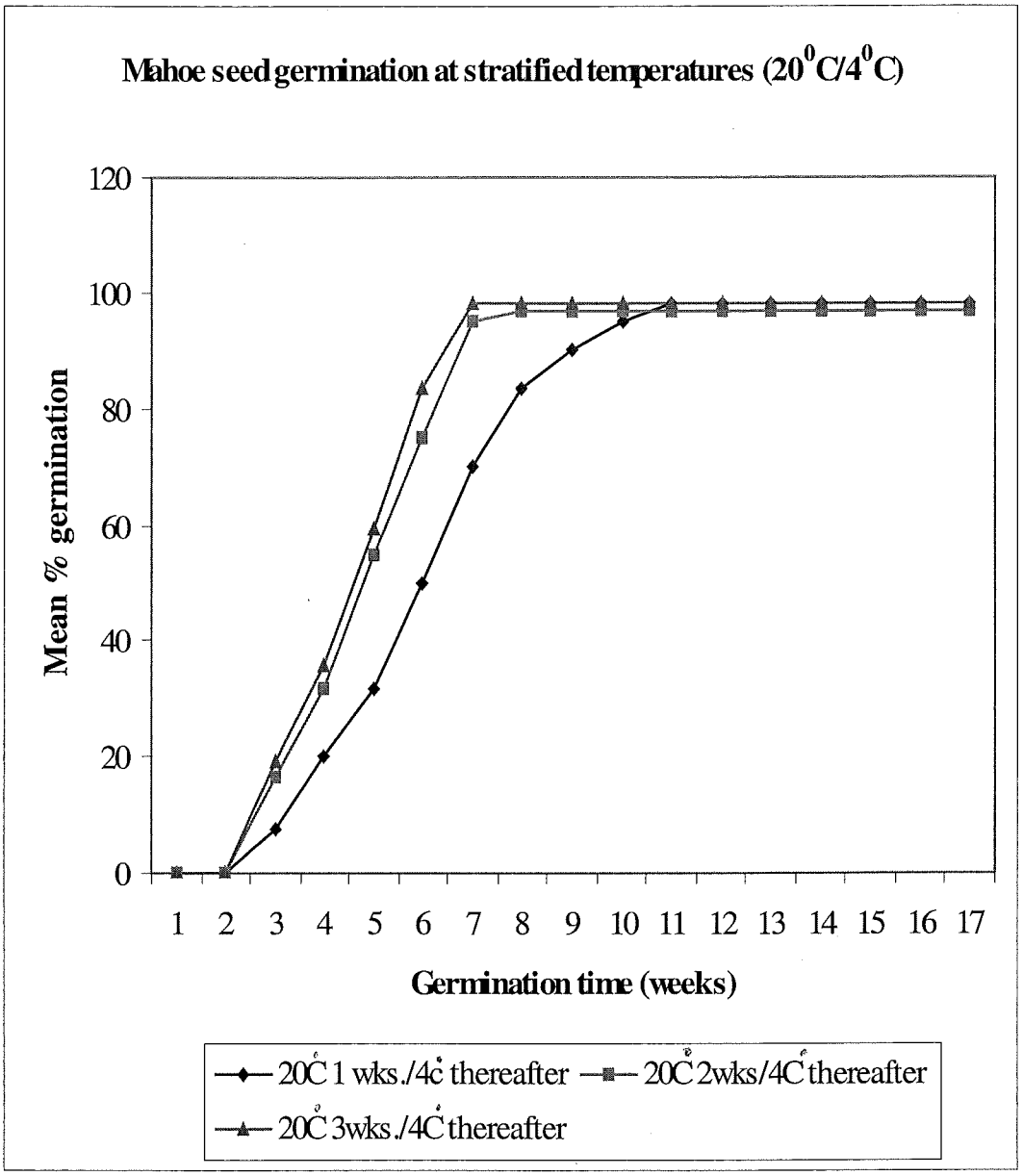


Figure 4.5 (b). Mahoe seed germination at stratified temperatures: $20^0C/4^0C$ temperature- initial warm period of 1, 2, 3 weeks.

4.6.3. Discussion

Elder seed germination significantly increased after temperature stratification although some germination was possible without stratification. Seeds in the control germinated very poorly with a mean percentage of 3.3 at the end of 20 weeks period. Elder germinated most successfully (60% maximum germination) when subjected to 20^0C for 8 weeks followed by a cold phase of 4^0C. Despite the slight reduction in final germination, no statistically significant effect was found for a second warm phase on seed germination of elder. Tylkowski (1982) found somewhat similar results, noting that germination capacity was markedly increased by the warm-followed-by-cold stratification, whether or not this treatment was followed by a second warm period. However, Roxburgh (1992) reported that elder required a warm (20-30^0C) moist stratification for about 60 days followed by a cold stratification for 90-150 days followed by a further warm (20-30^0C) moist period to give a maximum total germination of 65%.

The requirement by elder for temperature stratification prior to germination could be regarded as a disadvantage in the early stages of a succession. It takes approximately 1 year for a seed to overcome dormancy. However, clusters of elder patches visible in the Hoon Hay Valley disprove such a drawback. Moreover, as a long-lived, woody species, with a viable soil seed bank, elder's one year delay in germination should not be a problem. Another possibility is that breaking of dormancy in elder could be induced by the passage through birds; seeds found in bird droppings might be ready to start germination as soon as other essential requirements are met. However passing through a possum gut did not initiate germination (O'Cain 1997).

Mahoe seeds did not show any significant difference in germination when subjected to temperature stratification; this species does not require temperature stratification for successful germination.

4.7. Response to light

4.7.1. Methods

Seeds which had been stored for 3 months were used for this experiment. Seeds were soaked in distilled water for 48 hours, during which the soaking water was changed every 12 hours. Following two treatments were used:

1) 20 seeds from each species were placed in petri-dishes (with 5 replicates) and given a 24-hour dark period at 65 % relative humidity at 20^0C. The petri-dishes containing seeds on two moistened filter papers, were wrapped with two layers of aluminium foil and maintained under growth cabinet conditions for 60 days. Petri-dishes were observed every third day by opening them very briefly under low intensity (approx. 5 μ mol m^{-2} sec^{-1}) green light for about 3 minutes.

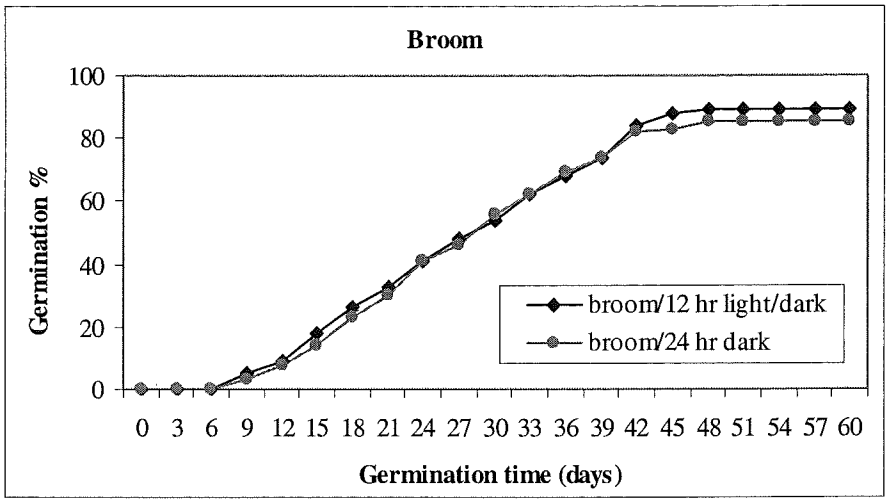
2) 20 seeds from each species (with 5 replicates) were treated with a 12 hr light period at 60% relative humidity (20^0C) followed by a 12 hr. dark period at 65% relative humidity at (10^0C) in a growth cabinet for 60 days. Germinated seeds were counted and removed from the experiment. These temperatures were chosen as they are similar to those experience in the field in early summer. The light levels in the growth cabinet was monitored using LI-COR quantum light sensors and read through a CR21X datalogger. The white fluorescent light provided in the growth cabinet was approximately 35 mol m^{-2} day^{-1}. Even though this illuminance level may not compare with natural conditions, the international seed testing association recommends 20 μ mol m^{-2} sec^{-1} of white fluorescent light as sufficient for studying light requirement for germination. According to Baskin and Baskin (1998), one or two 20W cool white fluorescent tubes 15-20 cm above will provide enough light for germination.

4.7.2. Results

Only broom and mahoe germinated in the trial. As elder failed to germinate during the experimental period it was excluded from the analysis. However, elder seeds left under the same experimental conditions for a further 4 months did exhibit a very low germination rate. Five elder seeds from the complete dark treatment and 7 seeds from 12 hour lighted treatment germinated out of 100 (from all 5 replicates).

The germination of broom was slightly increased in the light treatment than in the dark after approximately 42 days, whereas mahoe germination increased in the lighted treatment after approximately 39 days. The mean final germination percentage was greater in the lighted treatment than in the 24 hours darkness treatment, with a 4% increase in broom and a 9% increase in mahoe (Figure 4. 6 a & b). Analysis of variance of the treatment effect showed that light had no significantly different effect on seed germination of either broom or mahoe.

a)



b)

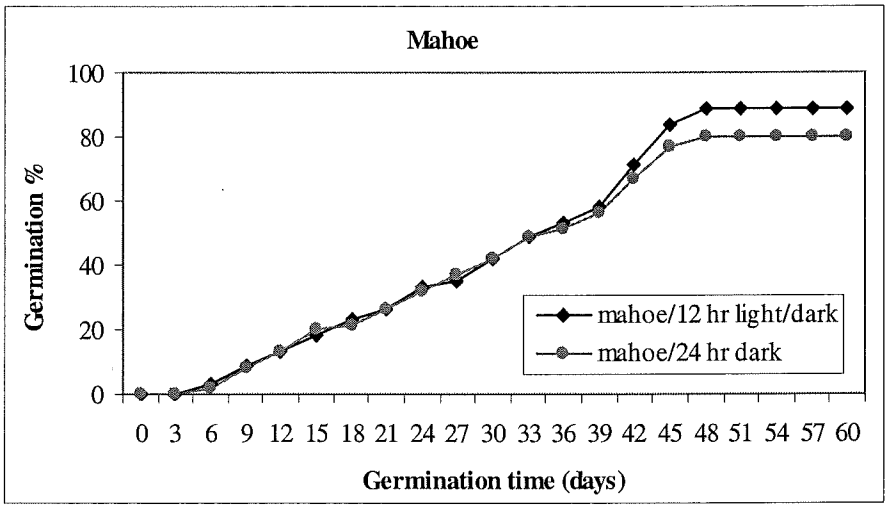


Figure 4.6. The influence of light on seed germination of a) broom and b) mahoe.

4.7.3. Discussion

Broom is able to germinate in the dark, and germination percentages did not differ significantly from lighted treatments. These results agree with work by Smith and Harlen (1991), who found of 17-31% germination for broom under natural day lengths; continuous darkness had no effect on germination rate over 22 days. In the present experiment broom showed 33% germination in the light and 30% germination in total darkness after 21 days (Figure 4.5). Bossard (1993) also reported at least 34% germination in broom regardless of light over 32 days. These results

suggest broom is capable of germination and establishment even under low light levels. Williams (1981) found that broom seedlings were able to develop under reduced light. However, there was an absence of 1-2 year old seedlings beneath a broom canopy and regeneration was possible only when the canopy was disturbed (Williams 1983).

Mahoe showed a similar response to broom, where the effect of light on seed germination was not significantly different from that effect of complete dark treatment. There is however, some discrepancy in the literature regarding the light requirement of mahoe. For example Burrows (1993, 1995a) found 100% germination success of mahoe seeds in the dark. Mahoe is also mentioned as a species with a light requirement for germination (Enright and Cameron 1988; Partridge 1989). Therefore, it would be important to establish out whether exposure to a low light in a short period of time would affect the germination. For instance, some species are known to be stimulated to germinate by green light (Baskin and Baskin 1979) although green light is recommended for checking seed germination in darkness. Furthermore, the light requirement for germination may vary with temperature; constant or alternating (Thompson *et al.* 1977).

Although elder seeds did not show any signs of germination during the experimental period, seeds left in darkness for a prolonged period resulted in germination, suggesting elder has no light requirement for germination. However, they do undergo a prolonged period of dormancy. Roxburgh (1992) also reported that elder is capable of germinating in the dark.

The requirement by seeds for light in order to germinate could be considered as an adaptive response to emerging gaps in a vegetation (Colinvaux, 1986; Bradbeer 1988;Tilman 1988; Fenner 1992) and as a general characteristic of pioneer species (Fenner 1987). This feature limits seed germination in insufficient light levels especially under large canopies.

Although the requirement of light exposure for the initiation of germination may be considered as an adaptation to vegetation gaps, it may be equally advantageous for seeds to germinate independent of light, especially under canopies. Seed germination and seedling development may reflect a flexibility not found in species with a strict light requirement in the early stages. They may need to wait until gaps appear in the canopy. Alternatively, the requirement of light for seed germination and seedling establishment might be different in a particular plant. A 'no light requirement' for germination might not necessarily mean that the seedlings of that plant could survive under shade.

4.8. Response to planting depth

4.8.1. Methods

The soil depths that broom, elder and mahoe seedlings will emerge through was determined. Elder seeds were stratified (20^0C/4^0C); both broom and mahoe seeds were scarified by gentle rubbing on sandpaper as pre-treatments. Twenty seeds from each species were sown in plastic planting trays at depths of 0, 1, 3, 5, 7, 10 cm with three replicates giving a total of 60 seeds for each species at each depth. Each tray contained seeds placed at one depth only. A potting mix was prepared to give a particle size composition of 4-2 mm (33%), 2-0.8 mm (33%) and less than 0.8 mm (33%). This substrate was mixed evenly. For the 0 cm depth treatment, petri-dishes with moistened filter papers were used as a substrate. This experiment was carried out under glass-house conditions with a 20^0C/16^0C temperature and 16 hour light cycle. Emerging seeds were counted when the radicles had emerged from the soil surface.

4.8.2. Results

There was no seedling emergence by the three species tested when buried to 10 cm. Broom seeds were capable of emerging from up to 7 cm, although the emerging percentage was very low (1.6%) at 7 cm (Table 4.6). The final mean percentage

emergence for broom at other soil depths were 96% (0 cm), 88.3% (1 cm), 66.6% (3 cm) and 58.3% (5 cm) (Figure 4.7 a).

Elder seedlings did not emerge from either 7 or 10cm depths. A maximum emergence of 43% was achieved at 0 cm after 12 weeks. Final seedling emergence for elder at other soil depths were 31.6% (1 cm) , 20% (3 cm) and 3% (5 cm) (Figure 4.7 b).

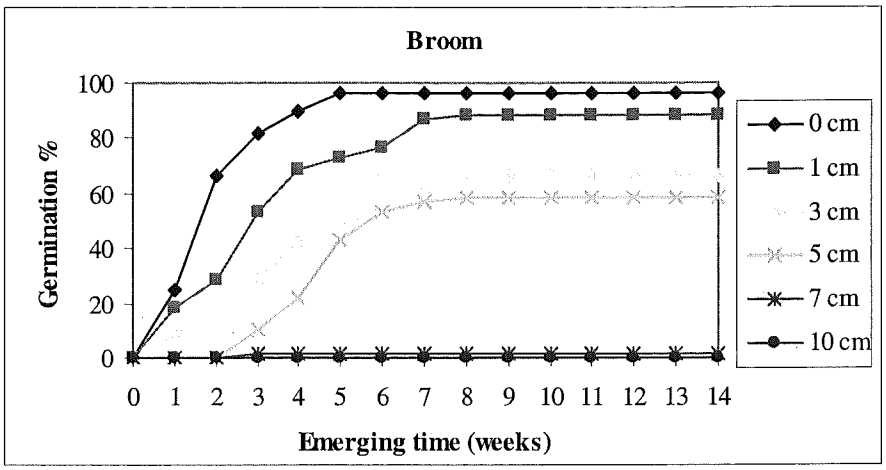
Mahoe seedlings did not emergence at depths lower than 5 cm. Mahoe reached maximum emergence at 0 cm (95%) after 8 weeks. As was found for broom and elder, emergence decreased with increasing soil depths, 1 cm (60%), 3 cm (30%) (Figure 4.7c).

Analysis of variance on final emergence percentages were highly significantly influenced by different species and depths ($F(2,36)=30.9$, $P\leq0.001$). Broom seedling emergence was significantly different between all soil depths, except 0 &1 cm, 3 &5 cm and 7 &10 cm depths (Tukey's test, $P\leq0.05$) (Table 4.6). Tests on elder and mahoe showed that seedling emergence was significantly different between all soil depths except 5 &7cm, 7&10cm, 5&10cm (Tukey's test, $P\leq0.05$) (Table 4.6).

Table 4.6. Seedling emergence at different depths. (Comparison of variable means indicated by the same letter are not significantly different (Tukey's test, $P\leq0.05$).

Depth (cm)	Broom		Elder		Mahoe	
	Mean	%	Mean	%	Mean	%
0	19.3 ± 0.3	96.7 a	8.6 ± 0.3	43.3 a	19 ± 0.6	95 a
1	17.6 ± 0.3	88.3 a	6.3 ± 0.3	31.6 b	12 ± 1.1	60 b
3	13.3 ±1.2	66.6 b	4.3 ± 0.3	21.6 c	6 ± 0	30 c
5	11.6 ±1.2	58.3 b	1 ± 0.6	5 d	0	0 d
7	0.3 ±0.3	1.6 c	0	0 d	0	0 d
10	0	0 c	0	0 d	0	0 d

a)



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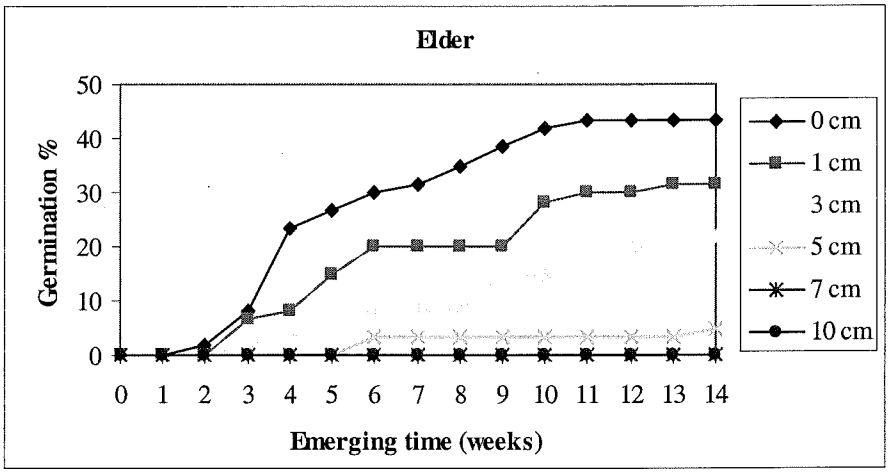


c)

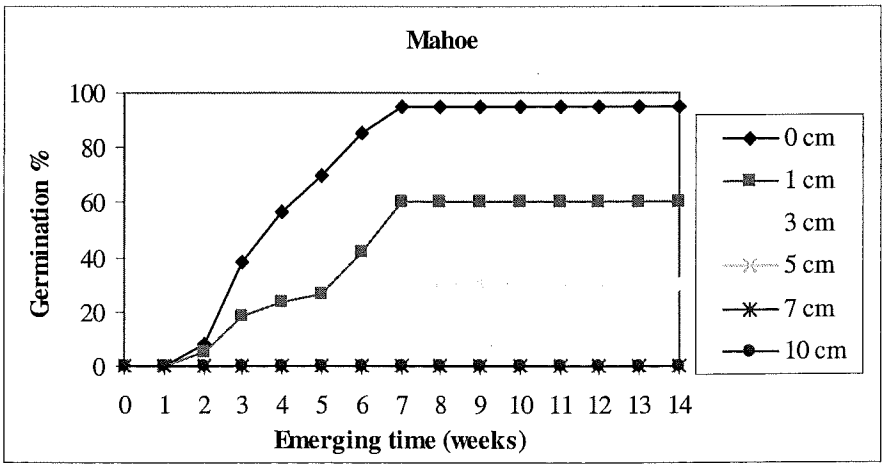


Figure 4.7. The influence of planting depth on germination of a) broom, b) elder and c) mahoe.

4.8.3. Discussion

Broom seeds were capable of emerging from deeper levels in greater percentages than elder or mahoe. Broom showed 58.3 % emergence even when at 5 cm depth. This result closely matches Bossard (1993), who reported 50% emergence for broom at 6 cm depth. The high emergence ability of broom from relatively deeper levels in soil increases the effectiveness of the soil seed bank. The longevity of viable seeds (Turner 1934) and an ability to emerge from deeper soil levels, places broom in a strong position as an early successional species. When disturbances occur in vegetation, the soil may also be disturbed (e.g. by uprooting of trees) which may increase the chances of seeds being buried.

The failure of elder and mahoe to emerge from below 5 or 3 cm respectively, suggests that although seeds of these species may be viable for long periods (Section 4.4.2), the importance of persistent in the soil seed bank could be relatively less than for broom. Although at least 90% of un-emerged mahoe seeds were rotten they had begun germination. This means even when the other "safe site" characteristics are met, mahoe seeds below 3 cm depth would not emerge, also indicating a lesser importance of the soil seed bank. Fenner (1987) suggested decreasing relative importance of a soil seed bank with the progression of a secondary succession.

4.9. Conclusions

1). Seeds of broom are well adapted to take advantage of the conditions during the early stages of a secondary succession. Although broom has relatively large seeds, a pod explosion mechanism together with secondary dispersal agents ensure wide dispersal of broom seeds. The large food reserve in heavier seeds increases the probability of establishment in a wide range of environments. The flexibility of broom to either germinate rapidly when fresh or following prolonged dormancy ensures a steady supply of seedlings over a long period of time; the plant has every opportunity to develop when all other conditions are met. Broom does not have a light requirement for germination, as would normally be expected from an early

successional species. The ability to germinate in the dark may be useful in less well-lit sites or when having to emerge from deeper levels in the soil.

2). Although a requirement of temperature stratification for germination is an adaptation to ensure seed germination at the right time of year, it has no significance as far as the successional status of elder is concerned. The contribution from seed characteristics for the successional status of elder is not as favourable as for broom. Elder seeds are less viable than either broom or mahoe. Even after temperature stratification, elder showed maximum germination of only 60%. However, the ability to remain viable for a number of years is an advantage as the soil seed bank supplies a continuous reservoir of seeds. However, only 5 % of seeds were capable of emerging from 5 cm. Germination, irrespective of light, can be an advantage where a standby population of seedlings under canopies awaits gaps. In this way, elder seedlings have a selective advantage above seeds which require light for germination.

3). Mahoe appears to be a species well suited for early to mid successional stages. The seeds have 100% viability when fresh and remain viable for several years, although there is some loss with time. Mahoe has the smallest seeds and is ready to germinate from fresh seeds or in the dark. That seeds can remain dormant for several years ensures an adequate supply of seeds at any time.

4). The seeds of broom, elder and mahoe all have versatile properties, enabling development into seedlings in either well-lit sites or under canopies, tolerating shaded conditions.

5). The three species possibly represent early succession to 'late early' or mid successional stages and the actual germination requirements seemed as less important seed attribute in determining successional positions of the three species as they all showed versatile properties. Perhaps dispersal mechanisms and methods of arriving into a new site may contribute more to the successional sequence than their germination requirements.

Chapter 5

The light and nutrient requirements of broom, elder and mahoe

5.1. Introduction

This chapter addresses the possible differences in light and nutrient requirements of broom, elder and mahoe. Background information is provided on light and nutrient requirements of plants during different successional stages. A description of the two experiments conducted to investigate the light and nutrient requirements of broom, elder and mahoe is followed by results and discussion. The two experiments described in this chapter address the second hypothesis set for the research, that differences in the light and nutrient requirements of broom, elder and mahoe influence their successional sequence.

5.2. Changes in resource availability during secondary succession

It is widely recognized that light and nutrient availability are dynamic factors, varying as result of changes in vegetation, and they have the potential to influence both primary and secondary successions. Colonizing species in a primary succession face low availability of nutrients and a high availability of light (Tilman 1988). Most primary successional sites start with virtually no nitrogen and high total phosphorus

levels in the parent material (often in apatite form), which needs to be broken down to release phosphate for colonizers (Vitousek and Walker 1987). Nitrogen availability increases through the succession with the help of nitrogen fixing organisms and total phosphorus declines (Walker and Syers 1976). This reduction in phosphorus in turn has implications for the availability of nitrogen (Walker and Syers 1976).

During the course of secondary succession, following a disturbance, rapid changes occur in resource supply and demand. The process of succession is associated with a general decline in the supply of resources and a concomitant increase in resource demand. Shortly after a disturbance, nutrient supply is generally increased and demand is reduced (Vitousek and Matson 1985). Matson and Boone (1984) studied patterns of nitrogen availability following natural disturbance of mountain hemlock forest in the Oregon Cascades and found nitrogen mineralization rates were at least doubled after the disturbance, but declined to the very low pre-disturbance rates as the stand regenerated. Matson and Vitousek (1981) studied nitrogen supply potentials following clear-cutting in the Hoosier National Forest, Indiana and found that nitrification was always greater in samples from clear-felled plots than controls. *In situ* incubations in that study indicated that higher soil temperature increased mineralization and nitrification rates in the most recently felled area. A study of phosphorus availability by Black and Marion (1984) also found similar results for nitrogen availability in Southern California.

The amount of light also increases immediately after a disturbance and decreases through the advancing succession (Vitousek and Walker 1987). Vegetation change in secondary succession involves a decrease in resource supply and increase in demand and at some stage, demand overtakes the supply and then in later succession, settles in to an equilibrium until another disturbance (Vitousek and Walker 1987). The implications of such changes in resource status influence colonization and species composition during the successional process.

In general, resource availability is at a maximum following a disturbance and therefore the plant species that reach these sites are able to grow rapidly. Later in succession, the demand exceeds the supply of resources and nutrient limitation is most likely to occur. At this point both the vegetation and forest floor are accumulating nutrients as decomposition is relatively slow and the most common limiting factor is nitrogen (Miller 1981).

Secondary successions can occur on soils that are sufficiently nutrient-rich that nutrients do not accumulate during succession but may actually be lost (Aarsen and Turkington 1985). Other secondary successions occur on nutrient-poor soils that have a period of nutrient accumulation much like that of primary successions (e.g. Inouye *et al.* 1987). Secondary succession on a nutrient-rich soil starts with a high availability of both nutrients and light. The dynamics of competitive replacement within a given habitat are strongly influenced by the maximal growth rates of the competing species. Within the constraints imposed by the availability of the limiting resources, the initial dominants in a newly disturbed, low plant density habitat are species with rapid growth rates. These are displaced by a series of species that have lower maximal growth rates but are increasingly superior competitors for the conditions of that habitat (Tilman 1988).

Horn (1971) examined the mechanism behind the relationship between light intensity and the growth rate of trees, and found that a mono-layered tree can grow rapidly in the sunlight, but not as quickly as a multi-layered tree. If both mono- and multi-layered trees simultaneously colonized a gap or other disturbed site, the multi-layered tree will grow faster to dominate until it is crowded by its neighbours. At this point the mono-layered tree gains a competitive advantage. In addition, if a mono-layered tree reaches a gap first, its shade prevents invasion of multi-layered species. If a multi-layered tree reaches a gap first it grows quickly but its under layer is open to invasion by mono-layered species. In this case the mono-layered species persist in the understory and eventually dominate.

5.3. Competition for nutrients and light in secondary succession

The determinants of which species will be successful in competition under different environmental conditions, and the importance of competition in determining species composition of plant communities have been the subject of considerable debate (Grime 1977; Tilman 1982, 1988). Resource competition is one process that influences colonization, transient dynamics and herbivory during succession (Tilman 1988). An explicit account of resource competition and the outcomes in plant communities was given by Tilman (1988). When several species are limited by a single resource, the one species with the lowest equilibrium resource requirement (R*) for the resource will competitively displace other species at equilibrium. R* is the amount of resource that the species must have in order to maintain a stable equilibrium population in a habitat. (Tilman 1982). The population size of the species with the lowest R* increases until that species reduces resource levels down to R*. At this level the resource availability is insufficient for the survival of other species and therefore these species would not survive. Measuring R* of different species at varying resource availability would predict which species would be the most efficient in tolerating resource limitations (Hsu *et al.* 1977; O'Brien 1974; Armstrong and Mc Gehee 1980).

The light and nutrient requirements of broom, elder and mahoe are not well documented in the literature. Williams (1981) mentioned that broom is a more successful competitor than gorse, especially on young highly mineral alluvial soils indicating broom's demand for nutrients. Roxburgh (1992) studied the relationship between light and regeneration ecology of elder in relation to distribution patterns of elder and documented its ability to grow well in shaded conditions. Tansley (1939) mentioned that elder seedlings were intolerant of heavy shade. However, there does not appear to have been any precise research on the light and nutrient requirements of these species. This chapter examines the relative demand of broom, elder and mahoe for light and nutrients in order to relate this to their position in the proposed successional pathway.

5.4. Materials and methods

5.4.1. Preliminary experiments

Several preliminary experiments were undertaken in order to chose appropriate light, N and P levels (a series of very low to very high levels). In a series of different shade levels tested, broom seedling growth was severely affected above 80% shade. Therefore, the light levels were selected as 100% light, (open), 50% light (50% shade) and 20% light (80% shade) of the light available in the glass-house (in a clear day the open treatment received an average maximum photosynthetic photon flux density is approximately 1000 μmol m^{-2} s^{-1}). Wooden shade frames covered with appropriate combinations of commercial shade cloths (30% and 50% shade cloths) were used to provide shade.

From the N and P levels tested, the very low and very high levels were excluded due to poor growth or toxicity. Selected N levels were 140 ppm (low), 210 ppm (medium) and 266 ppm (high). P levels were chosen as 15.5 ppm (low), 31 ppm (medium) and 46.5 ppm (high). For the remainder of this chapter the three N levels are referred as N1 (140 ppm), N2 (210 ppm) and N3 (266 ppm). Similarly the three P levels are referred as P1 (15.5 ppm), P2 (31 ppm) and P3 (46.5 ppm) while light levels are referred as L1 (100%), L2 (50%) and L3 (20%) of the light available in the glass-house. Hoagland's solution was used as the base for nutrient solutions and the specific concentrations were made accordingly.

During experiments, it was also noticed that broom had very poor growth if transferred from soil to growth medium before two weeks after germination. This was probably due to its inability to produce nodules under sterile perlite conditions. Assuming this, in Experiment 2 (light and nutrient trial), comparatively older seedlings with at least one visible nodule were used (approximately 4-6 weeks old seedlings). Nodulation was enhanced by inoculation when seedlings were in the soil. The light and nutrient requirements were tested in two separate trials. In the first

experiment, only the light requirement was examined, while in the second, both light and nutrient requirements were examined in seedlings grown in perlite.

5.4.2. Experiment 1: Light requirements of broom, elder and mahoe

5.4.2.1. Materials and methods

5.4.2.1.1. Seedling supply

Seeds of broom, elder and mahoe have considerably different requirements for germination. Therefore, different pre treatments were given at different times in order to obtain a uniformity of age and size of seedlings (see chapter 4). Seeds were placed in petri-dishes until germination began. The germinated seedlings were then transferred into planting trays with potting mix and raised for 2-4 weeks. Initial sampling involved ranking the seedlings from each species, according to their height, size, number of leaves and appearance. In order to obtain a supply of standard size seedlings, 20-30 seedlings ranked at the top of the scale as 'tall' seedlings were exempted. Similarly, the seedlings ranked as 'short' at the bottom of the scale were also discarded and only seedlings which fell within the middle rank of each scale were used. Selected seedlings were transplanted into 4 litre plastic pots containing potting mix. Each pot held two seedlings of the same species and these were grown on for a further week. Then fifteen pots from each species were randomly selected for the experiment. Measurements were averaged for the two seedlings in each pot.

5.4.2.1.2. Experimental Design and treatments

This experiment was conducted under glass-house conditions within a temperature range of 10-20^{0}C under natural light available in the glass-house. The experiment involved 3 species, 3 light levels and five replicates. Fifteen pots from each species were divided evenly into three groups and each group was allocated one light level: L1 (100%), L2 (50%) and L3 (20%). L1 treatment received natural sunlight in the

glass-house during the experimental period (September to November 1997); an average maximum photosynthetic photon flux density on a clear day was approximately 1000 μmol m^{-2} s^{-1}. Light treatments were made by covering wooden shade frames from different combinations of commercial shade cloths. Pots were watered regularly and randomly re-arranged after watering.

5.4.2.1.3. Measurements and calculations

- Five seedlings from each species were randomly sampled before the start of treatments in order to determine the initial dry weights.

- Seedling height was measured at the beginning of the experiment and weekly thereafter until the termination of the experiment.

- At the termination of the experiment after 12 weeks, seedlings were carefully uprooted, cleaned, dissected into root and shoot portions and dried at 80^0C for 48 hours to determine the dry weight.

Relative growth rate

The mean relative growth rates were calculated for whole plant and root and shoot portions for each species using Equation 5.1.

$$RGR = \frac{\log_e M2 - \log_e M1}{t2 - t1} \quad \text{.....Equation (5.1)}$$

Where: $\log_e M1$ is the natural logarithm of dry mass at time t1; and $\log_e M2$ is the natural logarithm of dry mass at time t2.

Root-shoot ratio, root-weight ratio and shoot-weight ratio

Biomass partitioning was determined by calculating weight ratios; root-shoot ratio (R/S), root weight ratio (RWR) and shoot weight ratio (SWR). The relationship between RWR and SWR is:

$$RWR + SWR = 1.$$

5.4.2.1.4. Data analysis

SAS univariate procedures (SAS Institute 1995) were used to check the normality of growth variables. Analysis of variance was conducted on all growth variables. SAS GLM procedures were used for analysis of covariance on growth ratios in order to remove any effects of initial plant size. When there were statistically significant differences means were further compared by Tukey's test. For derived variables (Root/ Shoot ratio, Root weight ratio and Shoot weight ratio) SAS univariate procedure was used to test normality. Regression analysis was performed using SAS REG procedure to analyse weekly height readings to check the relationship of height over time in different treatments. Regression analysis is performed when the magnitude of the dependent variable is assumed to be determined by the magnitude of the independent variable where as the reverse is not true (Zar 1984).

5.4.2.2. Results

5.4.2.2.1. Dry weights

Biomass production of different species under different light levels are illustrated in Figure 5.1. There were marked differences in biomass production of broom in response to light (Figure 5.1 a). Shoot biomass of broom was reduced by 17% (L2)

and 36.5% (L3) compared to L1 and total biomass was reduced by 18.5% (L2) and 37.5% (L3) compared to L1. The percentage reduction in broom root biomass production was 20 % (L2) and 39% (L3) compared to L1.

Unlike broom, elder responded differently to increasing shade by producing maximum biomass in L2 (Figure 5.1b). The shoot biomass was increased by 7% (L2) compared to L1 but showed almost no change in L3 compared to L1 (Figure 5.1b). Root biomass was also increased by 11% (L2) and decreased by 10% (L3) compared to L1. Total biomass of elder was increased by 9% (L2) and decreased by 4% (L3) compared to L1.

There were much less differences in biomass production of mahoe under different light levels (Figure 5.1c). Shoot biomass of mahoe was reduced by 6% and root biomass increased by 6% in L3 compared to L1. The reduction in total biomass was 1% in L3 compared to L1. However, root and total biomass were 20% and 11% lower in L2 than L1.

Statistical analysis of the main effects showed significant differences in all dry weight variables between species, treatments and interactions between species and treatments (species * treatments), except shoot dry weight between treatments and root dry weight between species*treatments (Table 5.1).

Table 5.1. The main effects of species and treatments on biomass variables.

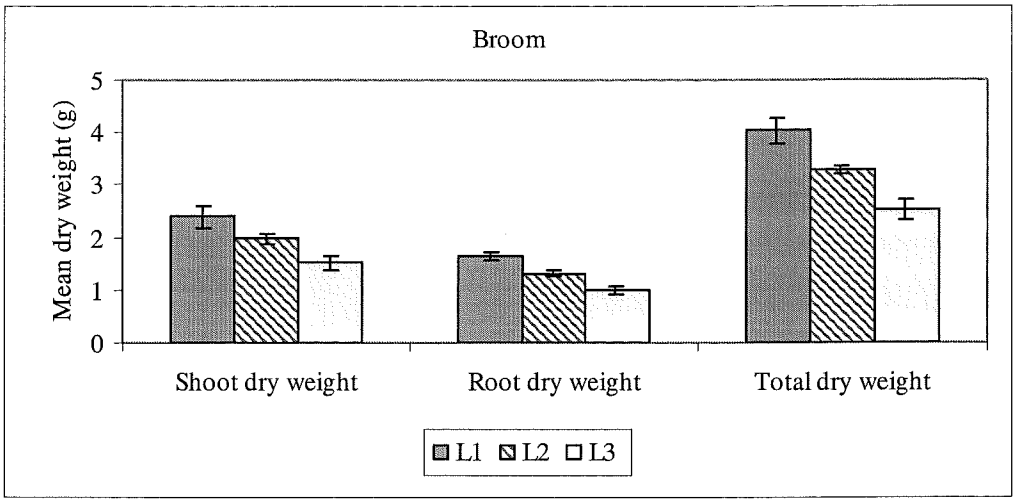
Source	DF	DW root		DW shoot		DW total	
		P value	F value	P value	F value	P value	F value
Species	2, 36	0.001	18.76	0.001	19.31	0.001	24.43
Treatment	2, 36	0.037	3.61	0.078	2.74	0.024	4.15
Spe* treat	4, 36	0.057	2.53	0.010	3.9	0.013	3.67

Further analysis using Tukey's test showed that all dry weight variables (root, shoot and total) were significantly different between broom & elder and elder & mahoe while differences were not significant between mahoe & broom (Table 5.2). The differences in broom root biomass and total biomass in response to different light levels were statistically significant between all light treatments (Tukey's test, $P \leq 0.05$) while difference in shoot biomass was significantly different only between light level 1 and 3 (Table 5.3). However, in the cases of elder and mahoe there were no significantly different effects of light treatments on any of the biomass variables (Table 5.3).

Table 5.2. Species level comparison of dry weight variables (root, shoot and total dry weight) of different species based on Tukey's test analysis. (* indicates that the comparisons between species are significantly different ($P \leq 0.05$). n.s= not significantly different ($P>0.05$)).

Variable	Species comparison	Significance
Root biomass	B-E	*
	E-M	*
	M-B	n.s
Shoot biomass	B-E	*
	E-M	*
	M-B	n.s
Total biomass	B-E	*
	E-M	*
	M-B	n.s

a)



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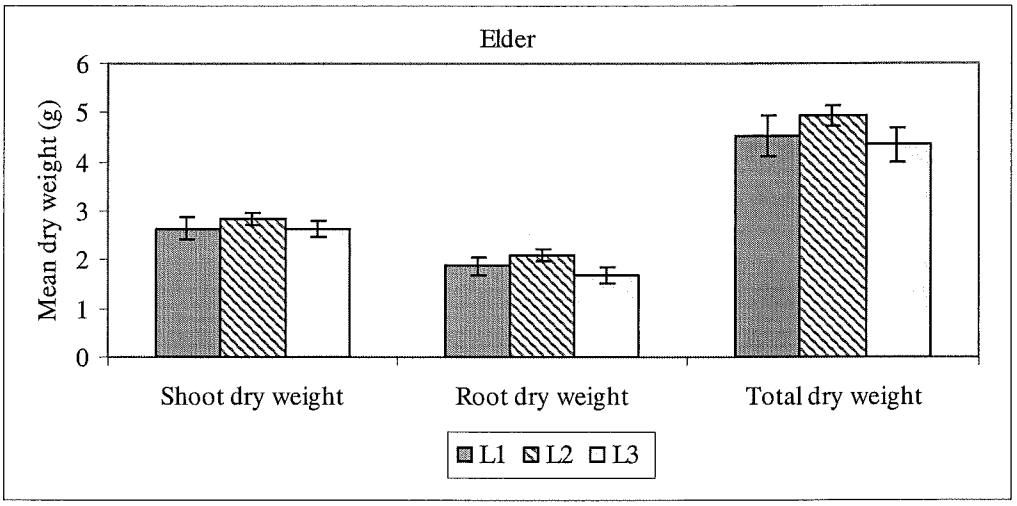

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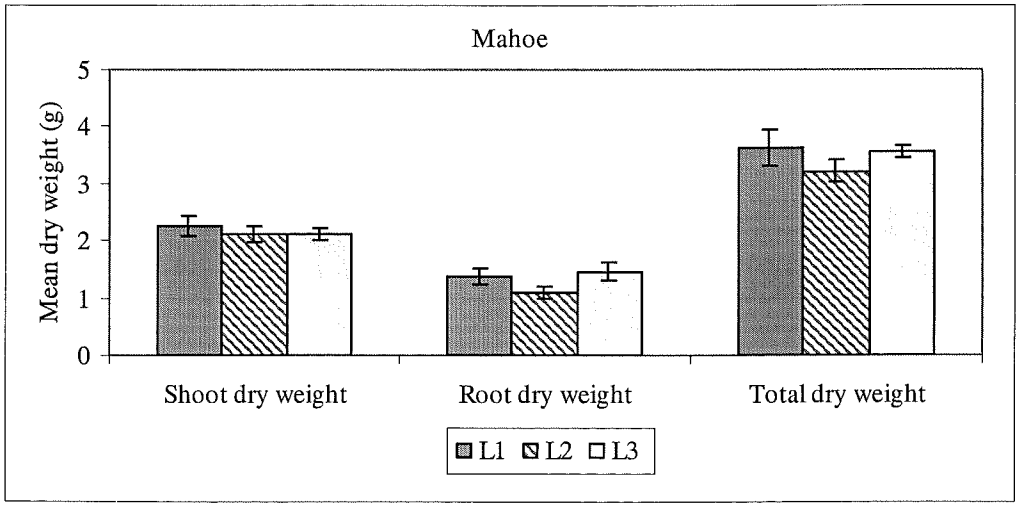


Figure 5.1. The dry weights of a) broom, b) elder and c) mahoe under different light treatments.

Table 5.3. Means (± SE) of dry weight variables for broom, elder and mahoe under different light treatments. (Means designated by the same letter are not significantly different (P≤0.05), based on Tukey's test analysis).

Variable	Treatment	Dry Weight (g)		
		Broom	Elder	Mahoe
Root biomass	L1	1.642± 0.08 a	1.879± 0.18 a	1.373± 0.04 a
	L2	1.312±0.06 b	2.088± 0.12 a	1.094±0.04 a
	L3	1.001± 0.08 c	1.689 ± 0.17 a	1.456± 0.03 a
Shoot biomass	L1	2.389± 0.21 a	2.644± 0.21 a	2.253±0.18 a
	L2	1.974±0.09 ac	2.841± 0.10 a	2.121±0.15 a
	L3	1.515±0.13 bc	2.649± 0.16 a	2.114±0.10 a
Total biomass	L1	4.031±0.25 a	4.522± 0.40 a	3.626 ±0.30 a
	L2	3.285±0.08 b	4.929± 0.19 a	3.215±0.20 a
	L3	2.516± 0.19 c	4.338± 0.33 a	3.570±0.10 a

5.4.2.2.2. Biomass partitioning

Broom SWR (shoot weight ratio) was increased by 2% in L3 compared to L1 while for elder and mahoe the increase in SWR was 3% and 8% respectively (Table 5.4). Both R/S ratio and RWR (root weight ratio) showed a trend to decrease in response to increasing shade even though the differences were not significantly different (Table 5.4). Figures 5.2 and 5.3 illustrate biomass partitioning of species in response to different light treatments.

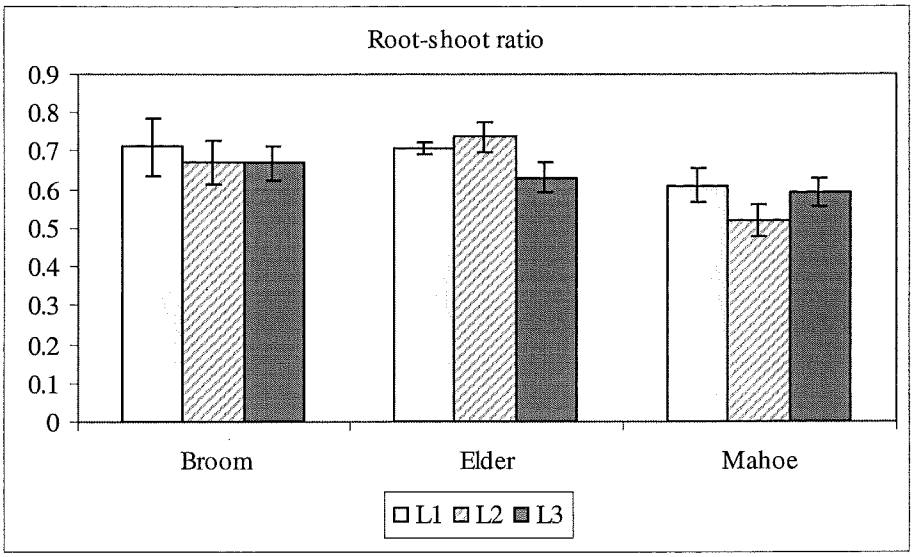


Figure 5.2. Root/Shoot ratios of broom, elder and mahoe in response to different light treatments.

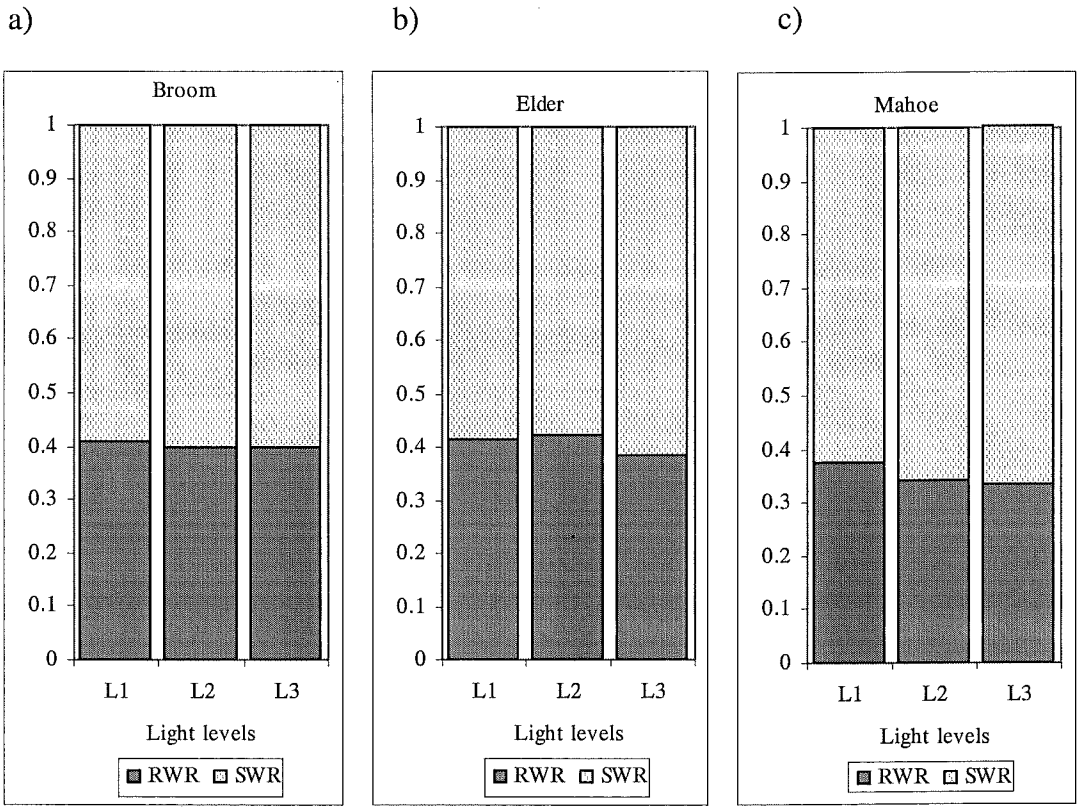


Figure 5.3. Root weight ratio and shoot weight ratio of a) broom, b) elder and c) mahoe in response to different light treatments.

Table 5.4. Root/shoot ratio, Shoot weight ratio, and Root weight ratio of broom, elder and mahoe under different light levels.

Species and Light levels	R/S	SWR	RWR
Broom			
L1	0.71±0.07	0.59±0.02	0.41±0.02
L2	0.67±0.06	0.60±0.02	0.39±0.02
L3	0.67±0.04	0.60±0.02	0.39±0.02
Elder			
L1	0.72±0.02	0.59±0.01	0.41±0.01
L2	0.74±0.02	0.58±0.01	0.42±0.01
L3	0.63±0.04	0.61±0.01	0.38±0.01
Mahoe			
L1	0.61±0.04	0.62±0.02	0.38±0.02
L2	0.52±0.04	0.66±0.02	0.34±0.02
L3	0.59±0.04	0.67±0.04	0.33±0.04

5.4.2.2.3. Seedling Height

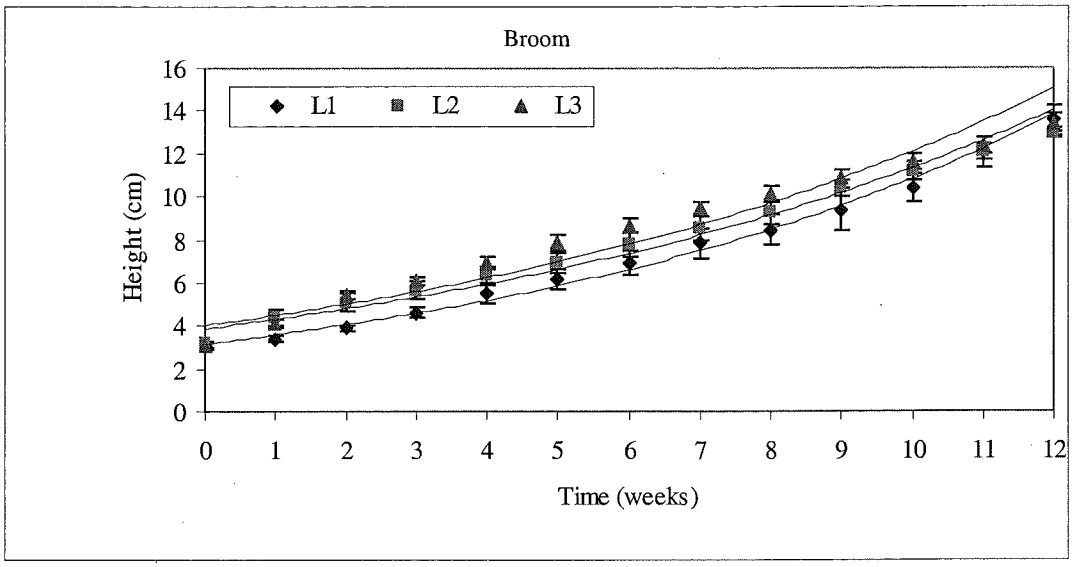
Final seedling height was significantly different between species ($F(2,36)=11.5$, $P\leq0.001$) with broom the tallest followed by mahoe and elder (Figure 5.4). Tukey's test for seedling height at species level showed significant differences ($P\leq0.05$) between broom and both elder and mahoe. Height differences between mahoe & elder were not significantly different. The effect of light treatments on the broom height was not significantly different between any of the treatments. Broom seedlings showed elongation of the inter-nodes with increasing shade (9% and 14% increase in youngest two inter-nodes in L3 compared to L1). In elder the treatment effect was significant only between L2 & L3. In mahoe, final seedling height was

significantly different between L1 & L3 while there was no significant difference of height in other light levels. Figure 5.4 shows growth curves of the species in different treatments. The results of a regression analysis, conducted to examine the nature of the relationship between seedling height and time in different species and treatments are presented in Table 5.5. The slope of the function of broom was not significantly different between treatments. Elder showed a maximum slope in L2 while mahoe showed maximum slope in L3.

Table 5.5. Regression analysis of height against time under different light levels showing estimates of intercepts (a) and slopes (b). (Figures shown are means ± SE).

Function parameters	L1	L2	L3
Broom			
a	2.26 ± 0.3	3.243 ± 0.20	3.501 ± 0.16
b	0.8459 ±0.04	0.787 ±0.03	0.822 ±0.02
r^2	0.86	0.92	0.95
Elder			
a	3.158± 0.14	2.63± 0.20	3.48 ±0.24
b	0.559±0.01	0.70± 0.03	0.54± 0.034
r^2	0.92	0.90	0.79
Mahoe			
a	3.313±0.100	3.45±0.19	3.297± 0.16
b	0.583 ±0.014	0.648± 0.027	0.760± 0.023
r^2	0.96	0.89	0.94

a)



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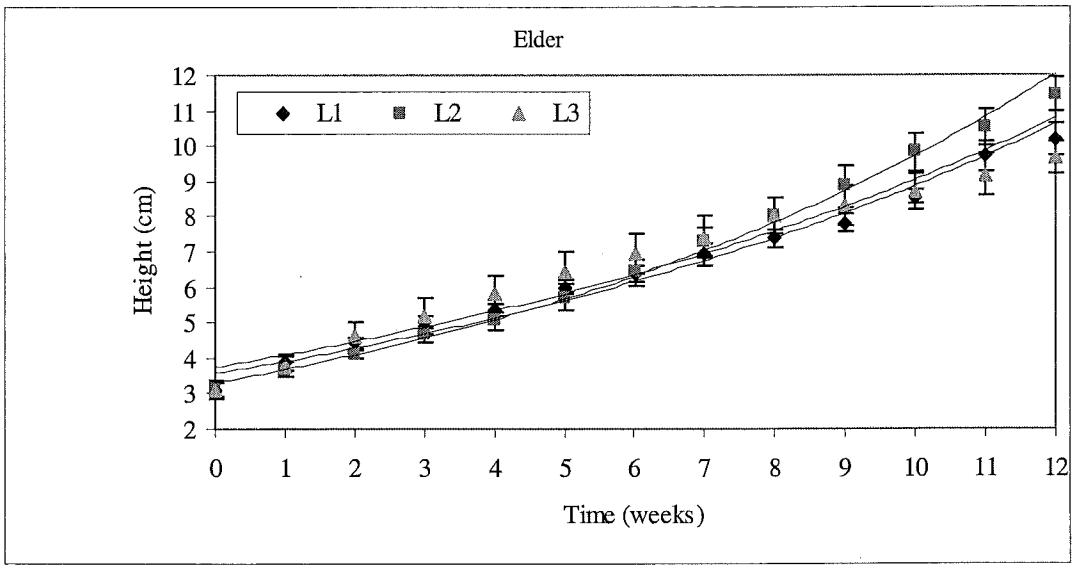

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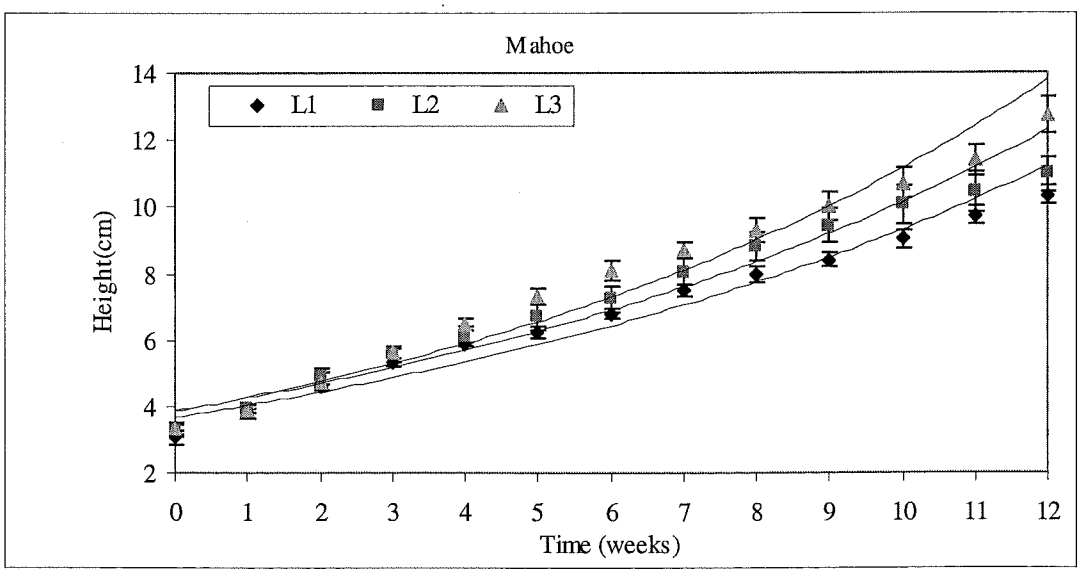


Figure 5.4. Growth curves of a) broom, b) elder and c) mahoe under different light levels.

5.4.2.2.4. Relative growth rate

The analysis of the main effects by SAS GLM procedures showed relative growth rate of shoot and total seedlings (RGR(shoot) and RGR(total)) were significantly different between species and treatments ($P \leq 0.05$). Species level comparison found significant differences ($P \leq 0.05$) in both RGR(shoot) and RGR(total) between broom & elder and broom & mahoe while RGR(root) was not significantly different between species (Table 5.6).

Table 5.6. Tukey's test results of species level comparison of relative growth rate. (* indicates the comparisons were significant at $P \leq 0.05$).

Variable	Species comparison	Significance
RGR(root)	B-E	n.s
	E-M	n.s
	M-B	n.s
RGR(shoot)	B-E	*
	E-M	n.s
	M-B	*
RGR(total)	B-E	*
	E-M	n.s
	M-B	*

The growth rate of broom was affected most by the different light levels compared to elder and mahoe. Broom RGR(shoot) reduced by 12% (L2) and 33% (L3) compared to L1. Similarly, RGR (root) reduced by 16% (L2) and 36% (L3) while RGR (total) reduced by 15% (L2) and 34% (L3) compared to L1. Analysis by Tukey's test showed that the reductions in both RGR(root) and RGR(total) were significantly

different between L1 & L3 and L2 & L3 (Tukey's test, P≤0.05) but not significant between L1 & L2 (Table 5.7). The reduction in RGR(shoot) of broom was significant between L1 & L3 (Tukey's test, P≤0.05) while there was no significant reduction between L2 & L3 or L1&L2 (Table 5.7).

The growth rate of elder shoots (RGR(shoot)) increased by 6% (L2) and 0.6% (L3) compared to L1. RGR(root) and RGR(total) of elder increased by 10% and 7% in L2 and decreased in L3 by 10% and 2% compared to L1. When considering mahoe, RGR(shoot) decreased by 4% (L2) and 3% (L3) compared to L1. RGR (root) of mahoe was reduced by 18% (L2) and increased by 5% (L3) compared to L1. Similarly, RGR(total) was reduced by 6% (T2) and increased by 2% (L3) compared to L1. However, the differences in relative growth rates of elder and mahoe under different light levels were not statistically significant (Table 5.7).

Table 5.7. Tukey's test results of treatment effect on growth variables of broom, elder and mahoe. (Means designated by the same letter are not significantly different at P≤0.05 for each treatment and each species).

Treatments	RGR(shoot)	RGR(root)	RGR(total)
	mg g^{-1} day^{-1}		
Broom			
L1	16.4 ± 1.2 a	16.4 ± 0.52 a	16.4 ± 0.78 a
L2	14.3 ± 0.54 ac	13.7± 0.57 a	14.0± 0.29 a
L3	10.9 ± 1.1 bc	10.4 ± 0.96 b	10.8± 1 b
Elder			
L1	17.4± 0.98 a	14.5± 1.2 a	16.1 ± 1 a
L2	18.4 ± 0.48 a	15.9 ± 0.69 a	17.3 ± 0.48 a
L3	17.5± 0.77 a	13.1± 1.4 a	15.7± 0.97 a
Mahoe			
L1	18 ± 0.91 a	14.5 ± 1.2 a	16.2 ± 0.95 a
L2	17.3 ± 0.84 a	11.9± 0.89 a	15.2 ± 0.74 a
L3	17.4 ± 0.57 a	15.2 ± 1.3 a	16.6 ± 0.35 a

5.4.2.3. Discussion

Both the biomass and growth rate of broom were significantly reduced with increasing shade, suggesting a light dependency of broom. A trend was noticed in broom to allocate more biomass to above ground parts under shaded conditions. Even though broom seeds were able to germinate irrespective of light (as described in Chapter 4), growth rates at the seedling stage appeared to be critical for establishment because dependency on light enables broom seeds to establish successfully only when a gap is created. Shade intolerance is a common feature in the juvenile stages of early successional species and this allows rapid establishment under the high light conditions in gaps or in open habitats (Hart 1988).

In contrast, both elder and mahoe showed a greater ability to tolerate lower light levels than broom as elder and mahoe biomass production was not significantly affected by different light treatments. This results suggest an ability to tolerate shade by these two species. Dungan's (1997) observations of large numbers of seedlings in the understorey supports shade tolerance of mahoe. However, Tansley (1939), reported that elder seedlings were intolerant of heavy shade. Although elder grew most favourably in the 50% light treatment (L2) the differences between light levels were not statistically significant thus cannot support Tansley (1939).

The postulated successional sequence is supported by the results of this experiment. As an early successional species, broom is best able to establish in a gap or a open site situation because of light dependent feature of its seedlings. The significant decrease in broom seedling growth under shade conditions further highlights the better performance of broom under light. Moreover, the biomass production and growth rate of both elder and mahoe were not significantly affected by the different light levels suggesting lesser dependence of light by those two species, suiting them to less well illuminated conditions.

Although this experiment considered the growth of broom, elder and mahoe in relation to variation in one single factor (light); in the natural environments these

plants face numerous factors. The interactive effects of two or more factors may well affect their relative resource requirements. Furthermore, a short experimental time could prevent real differences from manifesting themselves.

5.4.3. Experiment 2: The light and nutrient requirements of broom, elder and mahoe

5.4.3.1. Materials and Methods

5.4.3.1.1. Seedling supply and initial sampling

Seedlings were raised as for Experiment 1; germinated seedlings were transferred into planting trays with potting mix and raised for 3-5 weeks. In order to enhance nodulation, broom seedlings were maintained in planting trays for an additional week prior to transplanting into perlite.

Seedlings of each species were ranked according to their size, height, number of leaves and appearance. In order to obtain a supply of standard size seedlings, twenty to thirty seedlings ranked at the top of the scale as 'tall' seedlings were exempted. Similarly, the seedlings ranked as 'short' at the bottom of the scale were also discarded. One hundred and eight middle-sized seedlings, with a healthy appearance, of each species were chosen for the experiment. Another five middle sized seedlings from each species were randomly chosen to determine initial biomass. Several seedlings from each species were kept as backups. The seedlings were carefully uprooted, washed with distilled water three times and planted one seedling per pot in 1 litre plastic pots filled with perlite on ½ concentration of nutrient solution for one week prior to the commencement of treatments.

5.4.3.1.2. Experimental design and arrangement of pots

This experiment was set up as a split plot design. In this design each level of one factor is assigned to a whole plot within a block. Each plot is then subdivided into as many subplots as there are in the other factor, which are then randomly allocated to these subplots (Sokal and Rohlf 1981). The present experiment had 3 (light levels) x 3 (N levels) x 3 (P levels) x 3 (species) x 4 replicates. Four glass-house benches were used for this experiment so that each replicate occupied one bench. On every bench three light levels were randomly arranged; under each light level, 9 nutrient treatments were randomly arranged for the 3 plant species totalling 27 plants under each light level. Figure 5.5 illustrates the set up of Replicate 1 on Bench no 1. Each pot was individually numbered, according to the treatments. For example, pot # 11-111 represented the replicate 1, light level 1, N level 1, P level 1 of the species 1 while pot # 31-232 represented replicate 3 of light level 1, N level 2, P level 3 of species 2.

5.4.3.1.3. Treatments

Three levels of light, nitrogen and phosphorus were given as treatments. The three light levels were same as for Experiment 1; L1-100% light, L2-50% light and L3-20% light. The three nitrogen concentrations used were 140 ppm, 210 ppm and 266 ppm. The three phosphorus levels were 15.5 ppm, 31 ppm and 46.5 ppm. The proportions of other nutrients were kept as per Hoagland's solution. Stock solutions for each nutrient treatment are presented in Appendix 1. Freshly made nutrient solutions were added at the top of each pot every two weeks for the first six weeks and weekly thereafter. Excess water was drained by placing pots on a stand, before placing on the bench. All pots were covered with a black polythene in order to reduce evaporation. The experiment was terminated after 20 weeks.

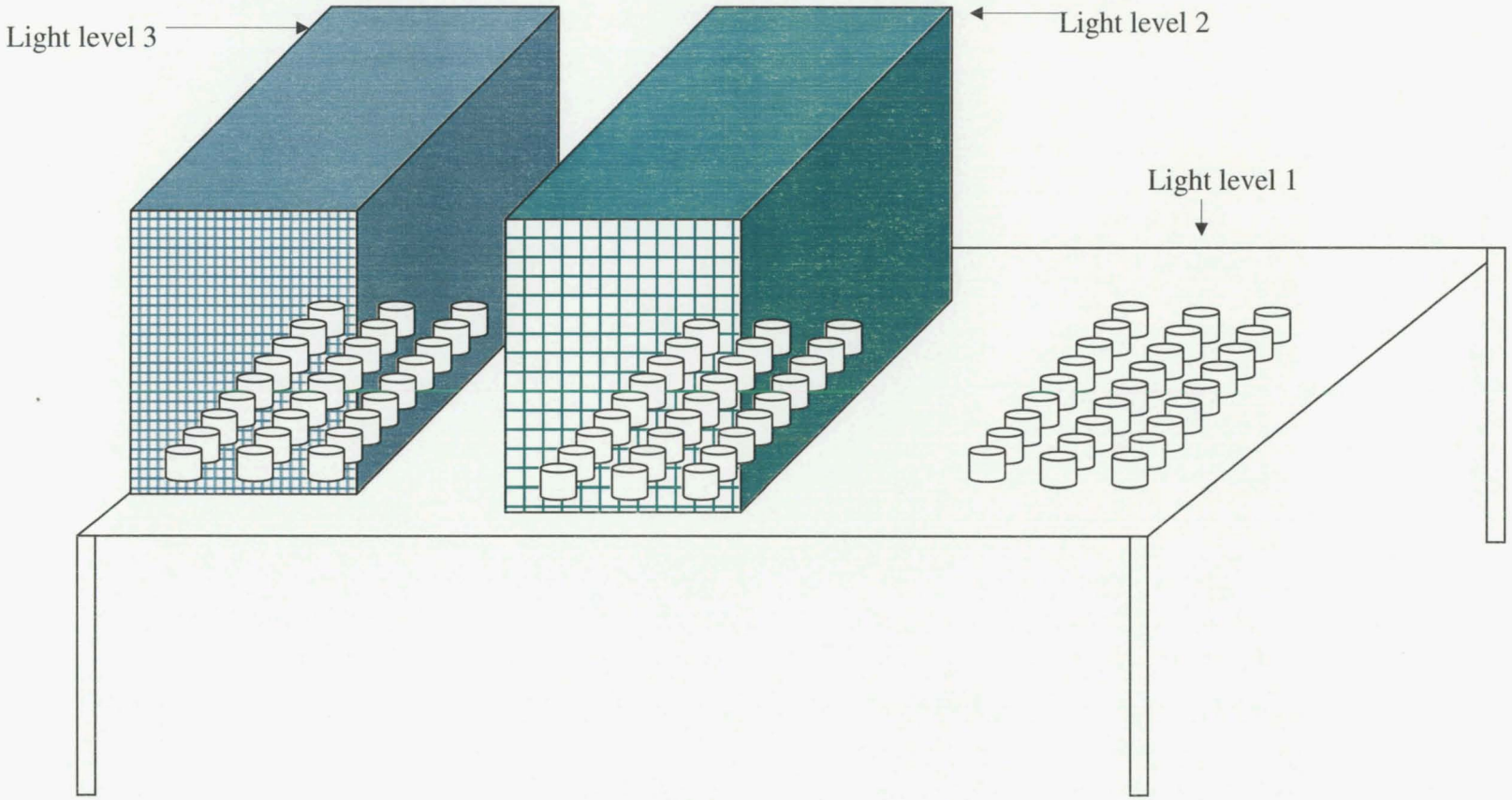


Figure 5.5. Diagrammatic representation of pot set up of replicate 1on Bench no 1 in the glass house

5.4.3.1.4. Measurements and calculations

1. Five seedlings from each species, randomly selected from the initial supply of experimental plants, were harvested and initial dry weights were determined.

2. Seedling height was measured at the start of the experiment and every 14 days thereafter until the experiment terminated.

3. At the termination of the experiment, the dry weights of root and shoot components were determined by drying plant material at 80^0C for 48 hours before weighing.

Regular height measurements were used to produce growth curves of the natural log of height against time to check the height growth under different treatments.

Relative growth rate was calculated according to the Equation 5.1, to compare the growth of different species under different conditions. Root-shoot ratio, root-weight ratio and shoot-weight ratios were determined to compare biomass partitioning between seedling components.

5.4.3.1.4. Data analysis

Data were evaluated by analysis of variance (ANOVA). SAS GLM procedure for analysis of variance in SAS/STATS 6.12, SAS Institute (1995) was performed on growth variables to check the main effects, i.e. whether there is significant differences of the explanatory variables (light, N,P, species) and their interactions, on response variables (shoot dry weight, root dry weight, root/ shoot ratio, total dry weight, relative growth rate, height). Significant differences of main effects were further analysed to see the effects of treatments at the species level and means were compared by the Tukey's test with a significance level of $P \leq 0.05$.

5.4.3.2. Results

5.4.3.2.1. Biomass

Table 5.8 presents a summary of statistically significant influences of explanatory variables on biomass variables. Results of main effects showed that there were significant effects of species, light, light*species (interactions between light and species) on all biomass variables (shoot, root, total) ($P \leq 0.001$). N showed a significantly different influence only on shoot and total biomass ($P \leq 0.001$). The main effect of P was significant only in shoot biomass ($P \leq 0.05$) although the interactive effect of P*species was significant on all biomass variables ($P \leq 0.05$). The interactive effect of N*P*species showed significantly different influence on shoot and total biomass ($P \leq 0.001$) and root biomass ($P \leq 0.05$) (Table 5.8).

Table 5.8. Significantly different main effects of explanatory variables on biomass variables. (Levels of significance as ***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$).

Biomass variable	Explanatory variable	DF	F	Significance
Shoot biomass	Light	2	49.3	***
	N	2	26.8	***
	Species	2	317.9	***
	Light*species	4	14.9	***
	N*P*species	8	6.9	***
	P	2	3.4	*
	P*species	4	3.2	*
	Light*N*P*species	16	1.9	*
Root biomass	Light	2	55.5	***
	Species	2	349.4	***
	Light*species	4	28.9	***
	N*P*species	8	2.5	*
	P*species	4	2.7	*
Total biomass	Light	2	73.9	***
	N	2	12.3	***
	Species	2	433.1	***
	Light*species	4	26.3	***
	N*P*species	8	5.5	***
	P*species	4	3.8	*

When considered at the species level broom, elder and mahoe responded differently in dry matter production to the effects of different light, N and P treatments. Shoot dry weight of broom decreased significantly ($F(2,81)=41.2$, $P\leq0.001$) with increasing shade towards L3 (Table 5.9, Figure 5.6a). Broom produced maximum shoot dry weight in L1N2P2 treatment while L3N1P1 yielded minimum dry weight (Figure 5.6a). Broom shoot dry weight was also significantly influenced ($P\leq0.001$) by N ($F(2,81)=8.6$) and P ($F(2,81)=9.2$) concentrations but the interactive effect of N*P was found to have no significant influence on shoot biomass of broom (Table 5.9). Tukey's test comparisons showed significant differences in shoot biomass between all light levels and levels 1&2 and 1&3 of both Nitrogen and Phosphorus.

Root biomass of broom was significantly influenced by light ($F(2,81)=14.7$, $P\leq0.001$) and P levels ($F(2,81)=6.1$, $P\leq0.05$). N treatments had no significant effect on root biomass. Tukey's test showed significant differences of root biomass between L1&L3, L2&L3 and P levels P1&P3 while all other comparisons were not significant.

Total dry weight of broom was highly significantly influenced ($P\leq0.001$) by light ($F(2,81)=56.6$), N ($F(2,81)=9.9$) and P ($F(2,81)=15.5$) concentrations. The influence of light on total dry weight of broom was significantly different between all light levels while the N effect was only significant between N1 & N3 and the effect of P was significant between P1 & P2 and P1 & P3 (Tukey's tests, $P\leq0.05$). Figure 5.6.a,b,c presents shoot, root and total biomass production under different treatments.

Elder biomass production (shoot, root and total) decreased with increasing shade except in the L2N3P3 treatment where shoot dry weight increased under light level 2 (Figure 5.7 a). Maximum root and total biomass production occurred in L1N2P2 treatment (Figure 5.7 b,c). Statistical analysis showed a highly significant effect of light ($P\leq0.001$) on shoot ($F(2,81)=28.9$) root ($F(2,81)=41.2$) and total ($F(2,81)= 45.9$) biomass (Table 5.9). Nitrogen had a significant effect only on shoot biomass ($F(2,81)=8.4$, $P\leq0.001$). N*P (interactions of N and P) had a significant effect on

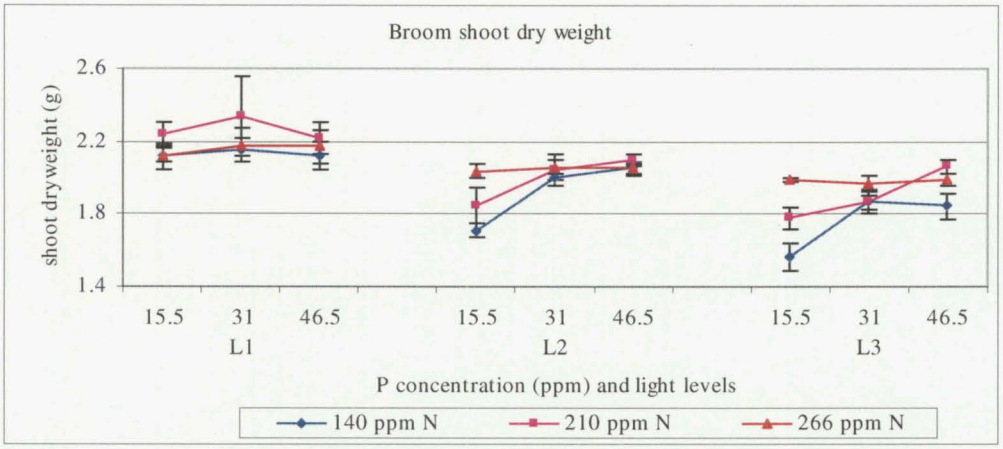
shoot biomass ($F(4,81)=7.1$, $P\leq0.001$) and total biomass of elder ($F(4,81)=4.3$, $P\leq0.05$) (Table 5.9). Tukey's tests showed that shoot biomass was significantly different ($P\leq0.05$) between L1&L3 and L2&L3; N1&N2 and N1&N3. Root and total biomass were significantly different between all light levels.

Mahoe produced maximum shoot biomass in L2N3P2, maximum root biomass in L1N2P1 and maximum total biomass in L2N3P3 treatment (Figure 5.8). Statistical analysis showed a significant effect of N on shoot ($F(2,81)=12.6$, $P\leq0.001$), and total biomass ($F(2,81)=10.2$, $P\leq0.001$) (Table 5.9). Interactive effect of N and P (N*P) showed a significant effect ($P\leq0.05$) on shoot ($F(4,81)=4.7$), root ($F(4,81)=4.9$) and total biomass ($F(4,81)=10.2$) (Table 5.9). All other variables did not show any significant effect. Shoot and total biomass production were significantly different between N1&N2 and N1&N3 while root biomass was significantly different between N1&N3 (Tukey's test, $P\leq0.05$).

Table 5.9. Significantly different effects of explanatory variables on biomass variables at species level as shown by SAS GLM. (Levels of significance are ***$P\leq0.001$, **$P\leq0.01$, *$P\leq0.05$).

variable	Broom	Elder	Mahoe
Shoot biomass	Light (***) N(***) P(***)	Light (***) N(***) N*P(***)	N(***) N*P(*)
Root biomass	Light (***) P(*)	Light (***)	N*P(*)
Total biomass	Light (***) N(***) P(***) N*P(*) Light*N*P(*)	Light (***) N*P(*)	N(***) N*P(*)

a)



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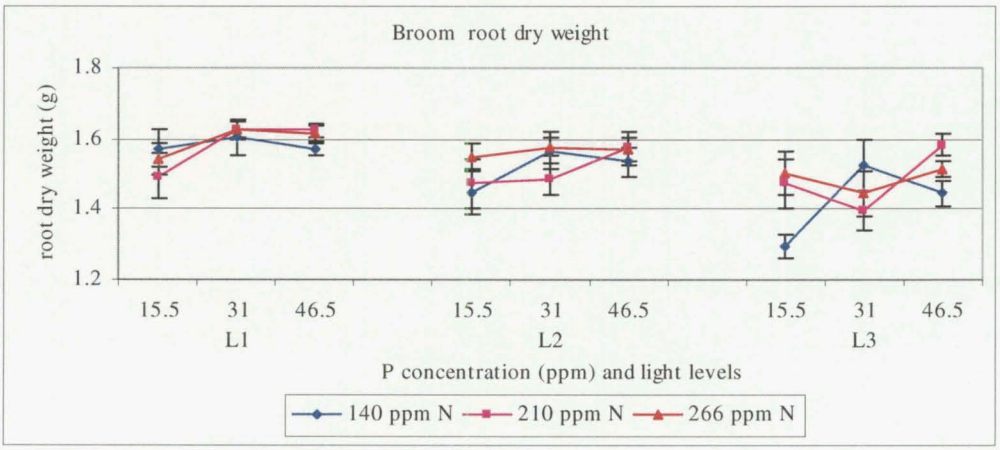

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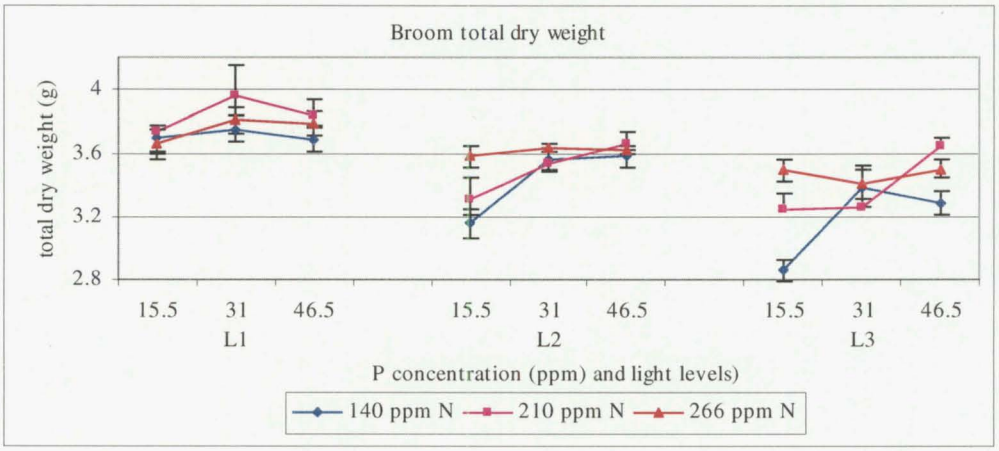
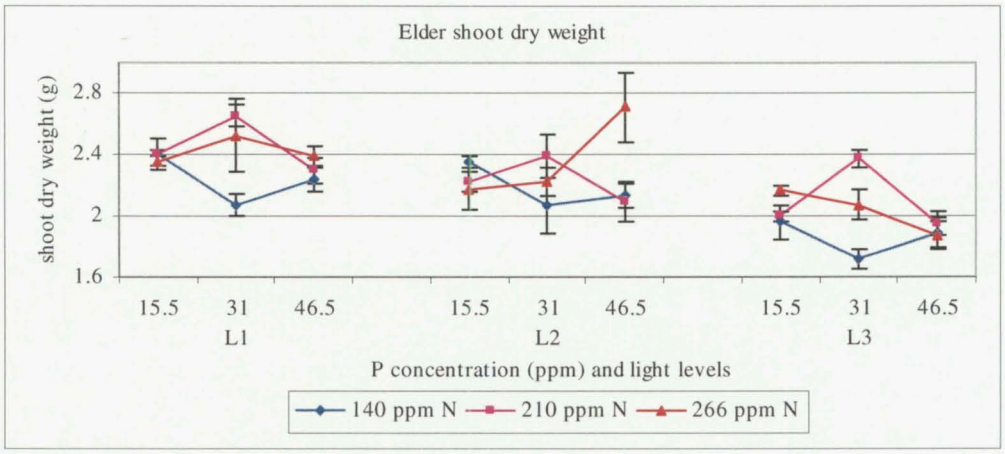


Figure 5.6. Biomass production; a) shoot, b) root and c) total of broom under different treatments.

a)



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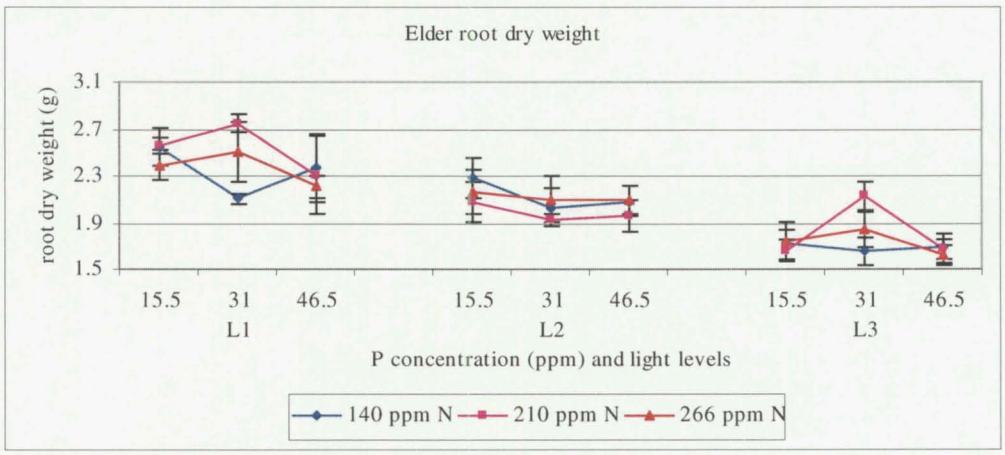

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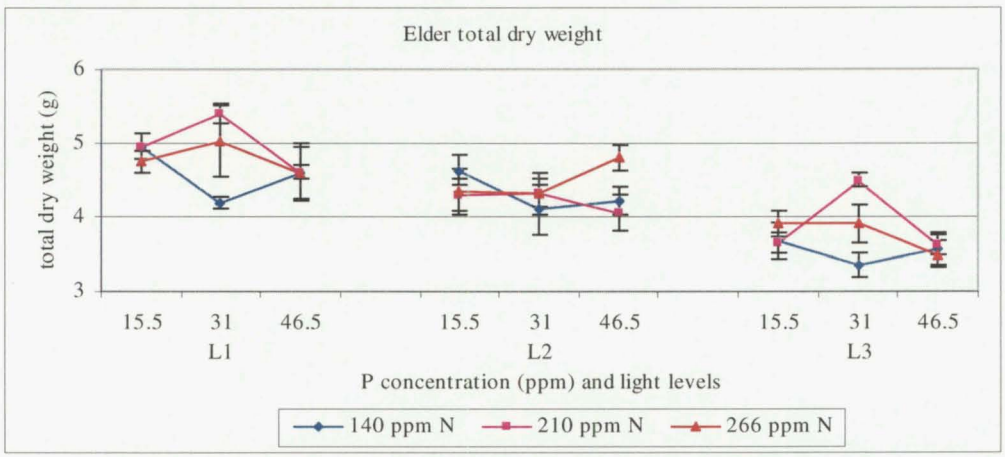
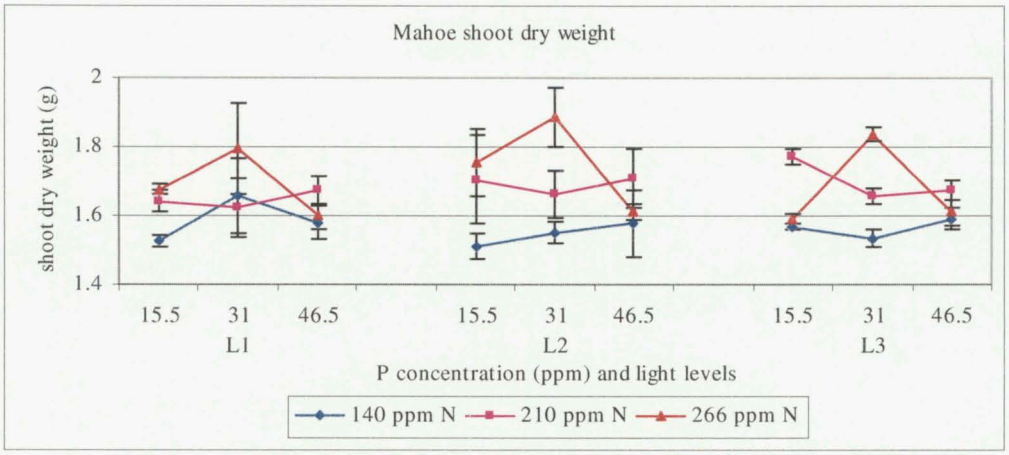


Figure 5.7. Biomass production; a) shoot, b) root and c) total of elder under different treatments.

a)



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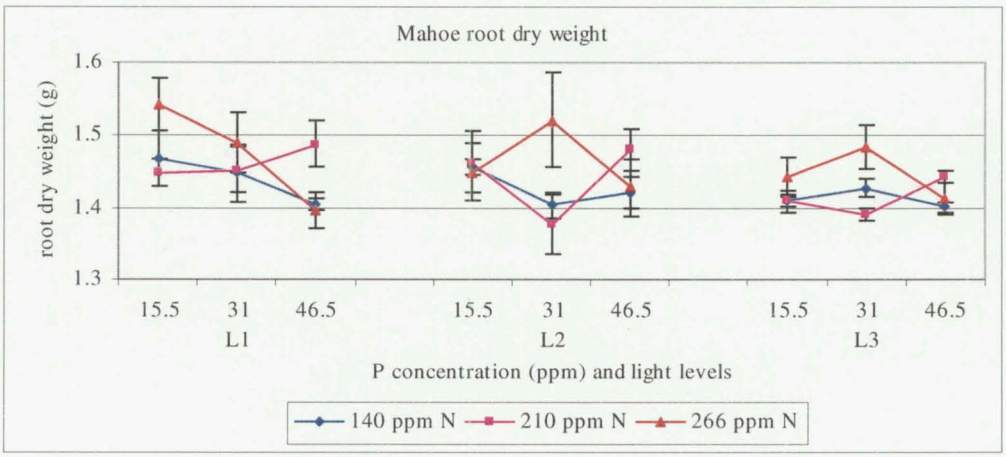

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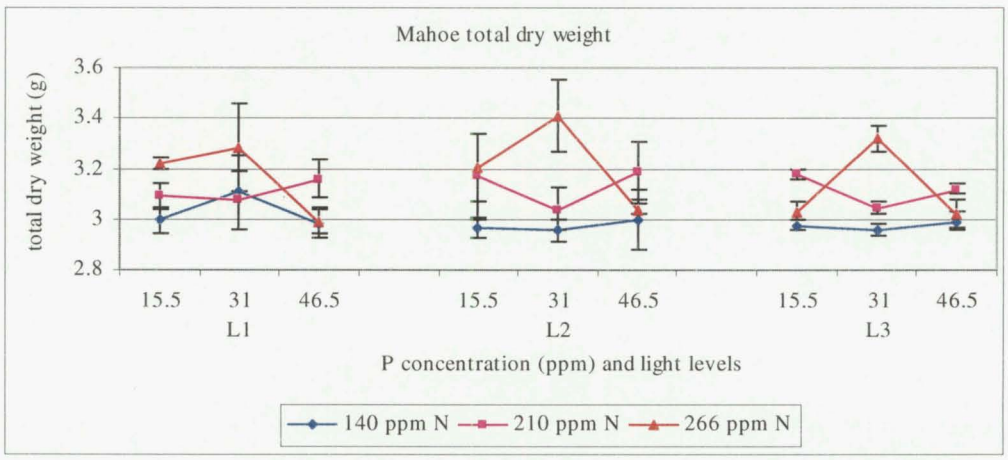


Figure 5.8. Biomass production; a) shoot, b) root and c) total of mahoe under different treatments.

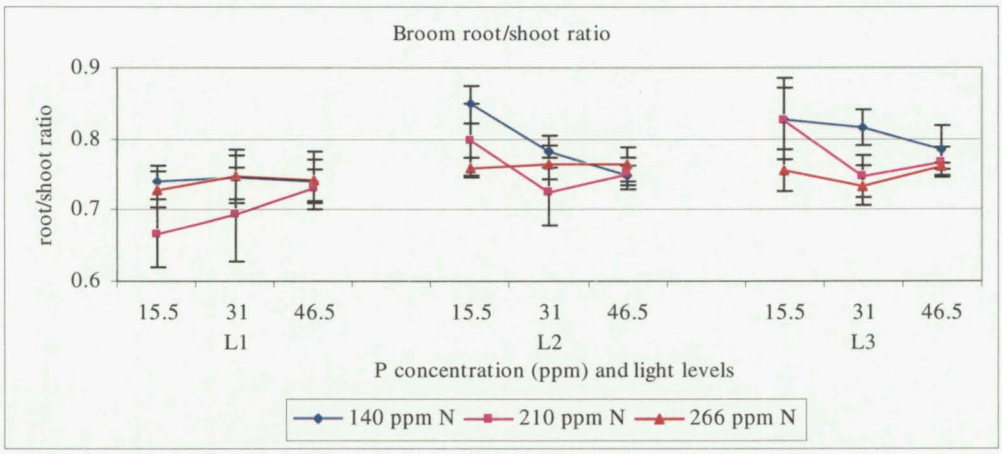
5.4.3.2.2. Biomass Partitioning

SAS GLM analysis showed Root/shoot ratio was significantly affected ($P \leq 0.001$) by nitrogen ($F(2,243)=11.7$), species ($F(2,243)=131.3$), light ($F(2,243)=6.4$) and interactions of species*light ($F(4,243)=13.5$).

At the species level, root/shoot ratio of broom was significantly increased with increasing shade (Figure 5.9.a). Root/shoot ratios of broom were significantly different between L1&L2 and L1&L3 (Tukey's test, $P \leq 0.05$). The effects of N, P and their interactions on R/S ratio of broom were not significantly different although root/shoot ratio showed a decreasing trend with increasing N and P concentrations (Figure 5.9 a).

In elder, there was significant effect of light on root/shoot ratio ($F(2,81)=14.9$, $P \leq 0.001$) (Figure 5.9.b). Comparison at different light levels showed significant differences between L1&L2 and L1&L3 (Tukey's test, $P \leq 0.05$). Both N and P levels had no significant influence on R/S ratio. When considering mahoe, root/shoot ratio was significantly decreased with increasing N concentrations ($F(2,81)=13.2$, $P \leq 0.001$) (Figure 5.9.c) while light and P levels had no significant influence. Nitrogen levels comparison showed significant differences between N1&N2 and N1&N3 (Tukey's test, $P \leq 0.05$).

a)



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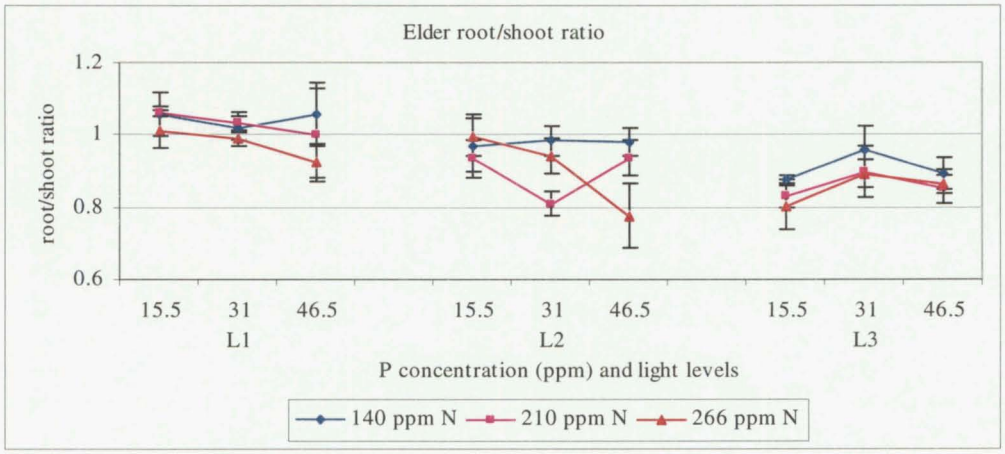

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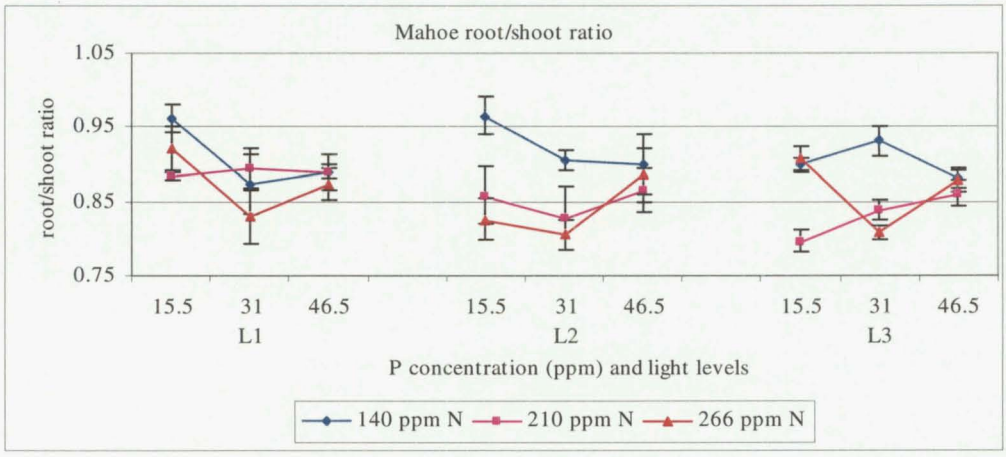


Figure 5.9. Mean root/shoot ratios of a) broom, b) elder and c) mahoe under different light, N and P treatments.

5.4.3.2.3. Relative growth rate

Figures 5.10, 5.11, and 5.12 represent the mean relative growth rate of the shoot, root and total plant of broom, elder and mahoe under different treatments. SAS GLM procedures were performed to see the effect of variables on the relative growth rate of shoot, root and total plant. Results showed a highly significant difference in RGR(shoot) between species ($F(2,243)=167.2$, $P\leq0.001$), light ($F(2,243)=48.2$, $P\leq0.001$), Nitrogen ($F(2,243)=31.5$, $P\leq0.001$), P ($F(2,243)=3.6$, $P\leq0.05$), species*light ($F(4,243)=14.6$, $P\leq0.001$) and species*P ($F(4,243)=4.3$, $P\leq0.01$) while all other variables were not significant. RGR (root) was highly significantly different ($P\leq0.001$) between species ($F(2,243)=133.7$), light ($F(2,243)=59.1$), species*light ($F(4,243)=24.3$), while other variables were not significant. RGR (total) was highly significantly different ($P\leq0.001$) between species ($F(2,243)=206.8$), light ($F(2,243)=76.2$), N ($F(2,243)=15.7$), species*light ($F(4,243)=23.5$).

Species level analysis showed the growth rate of broom and elder were significantly affected by light while mahoe growth rate was not significantly effected by light. Nitrogen had a significant effect on the growth rates of all three species while phosphorus significantly affected the growth rate of broom (Table 5.10).

Table 5.10. Significantly different effects of explanatory variables on relative growth rate of broom, elder and mahoe. (Levels of significance as *** $P\leq0.001$, **$P\leq0.01$, * $P\leq0.05$).

Variable	Broom	Elder	Mahoe
RGR (shoot)	light(***) N(*) P(*)	light(*) N(*)	N(***)
RGR (root)	light(*) P(*)	light(*)	-
RGR (total)	light(***) N(*) P(*)	light(***)	N(*)

The treatment effects were further analysed using Tukey's test to examine the effect of different levels of treatments on the relative growth rate. Broom RGR (shoot) decreased markedly with increasing shade from L1 to L3 (Figure 5.10). Statistical comparison of light levels showed that the broom RGR (shoot) was significantly different between all light levels (Tukey's test, $P \leq 0.05$). Broom showed higher growth rate, (the shoot portion in particular) under all N and P levels when light is at its maximum (Figure 5.10) highlighting the importance of light. Both N and P comparisons showed a significant difference between levels 1 & 2 and 1 & 3 (Tukey's test, $P \leq 0.05$).

Broom RGR(root) was lower than RGR (shoot) especially in light level 1 (Figure 5.10). The light level comparison of broom RGR (root) showed significant differences between light levels L1 & L3 and L2 & L3 while light level L1 & L2 was not significantly different. There were no significant differences between any of the N levels. P comparisons showed a significant difference between P levels 1 & 3. The RGR (total) was maximum in L1N2P2 followed by L1N2P3, L1N3P2 and L1N3P3 respectively. RGR (total) was significantly different between all light levels while for Nitrogen levels it was significantly different between levels N1 & N3 (Tukey's test, $P \leq 0.05$). P comparisons showed a significant difference between P1 & P2 and P1 & P3 (Tukey's test, $P \leq 0.05$).

Elder had the highest relative growth rate of all three species. Fast growth was evident for both root and shoot portions. Maximum growth rate was recorded in L1N2P2 treatment (Figure 5.11). Growth rate of elder decreased with decreasing light, with minimum growth rate in thelowest light level treatment (Figure 5.11). Growth rate was at its minimum at L3 irrespective of nitrogen and phosphorus level except in the treatment N2P2 treatment where the growth rate was minimum at L2 (Figure 5.11). Tukey's tests showed that relative RGR(shoot) was significantly different between light levels L1 & L3 and L2 & L3 ($P \leq 0.05$). Nitrogen comparisons showed significant differences between N levels N1 & N2 and N1 & N3 ($P \leq 0.05$). RGR(shoot) was not significantly affected by different P levels. Relative growth rate

of roots of elder decreased from L1 to L3 (Figure 5.11). RGR(root) was significantly different between all light levels ($P \leq 0.05$), while there was no significant effect of N and P. RGR(total) also showed a significant differences between all light levels while nitrogen levels and P levels comparisons showed no significant difference.

Mahoe showed higher growth rates under intermediate light conditions (L2, L3) than L1 (Figure 5.12). Highest growth rate was recorded in L2N3P2 treatment followed by L3N3P2 (Figure 5.12). Mahoe showed more dependence on higher nitrogen levels than the other species, with maximum growth rate at N3 concentrations followed by N2 and N1. N seemed more important to the growth of mahoe because at L3 mahoe showed less growth rate when N concentration is low (N1) irrespective of P levels (Figure 5.12). Statistical comparisons, however, showed that the differences in relative growth rate of shoot, root and total plant were not significant between different levels of light or P. Both RGR(shoot) and RGR(total) were significantly different between N1 & N2 and N1 & N3 while different N levels did not significantly affect RGR(root).

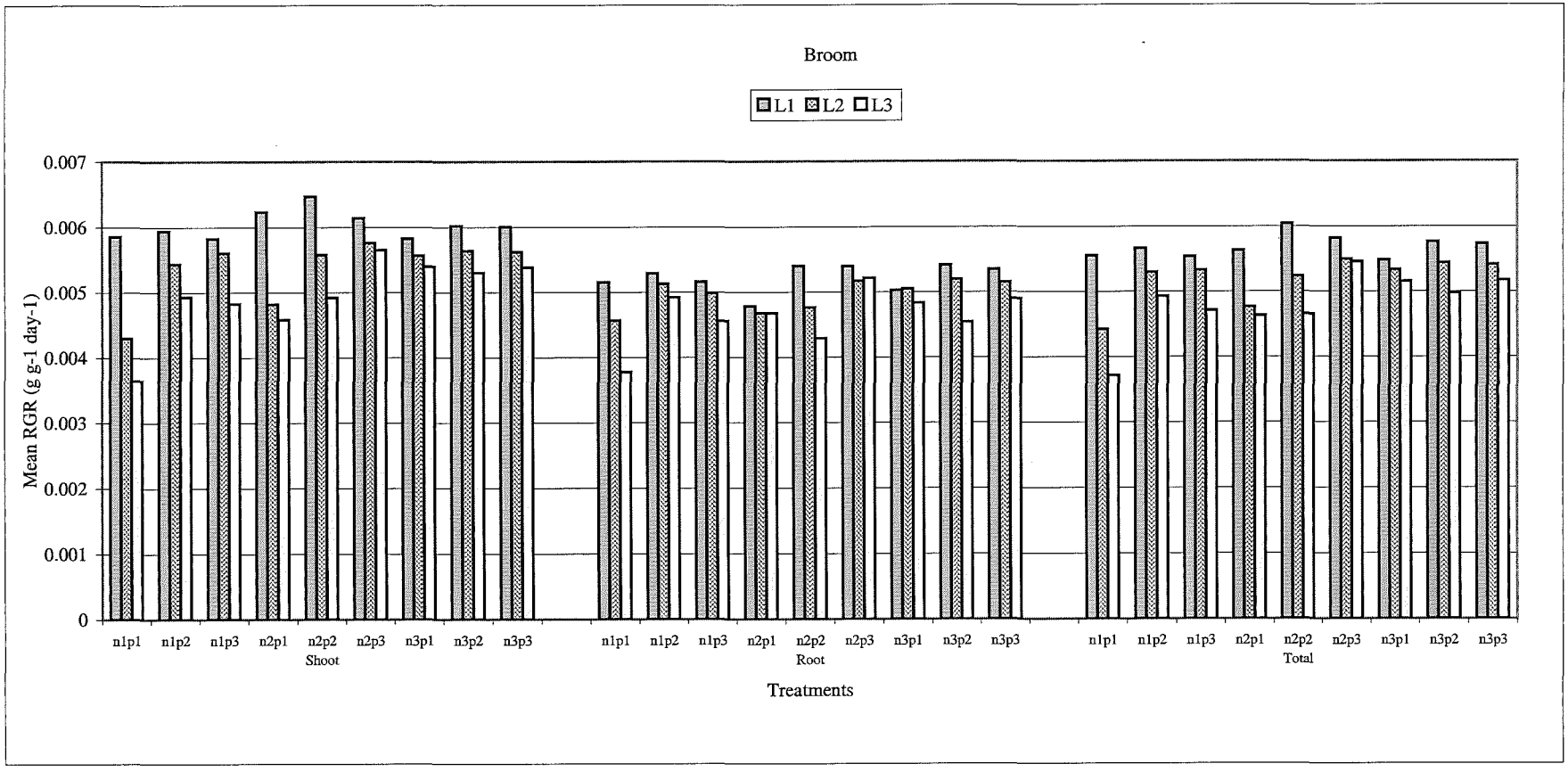


Figure 5.10: Mean relative growth rate of broom under different treatments

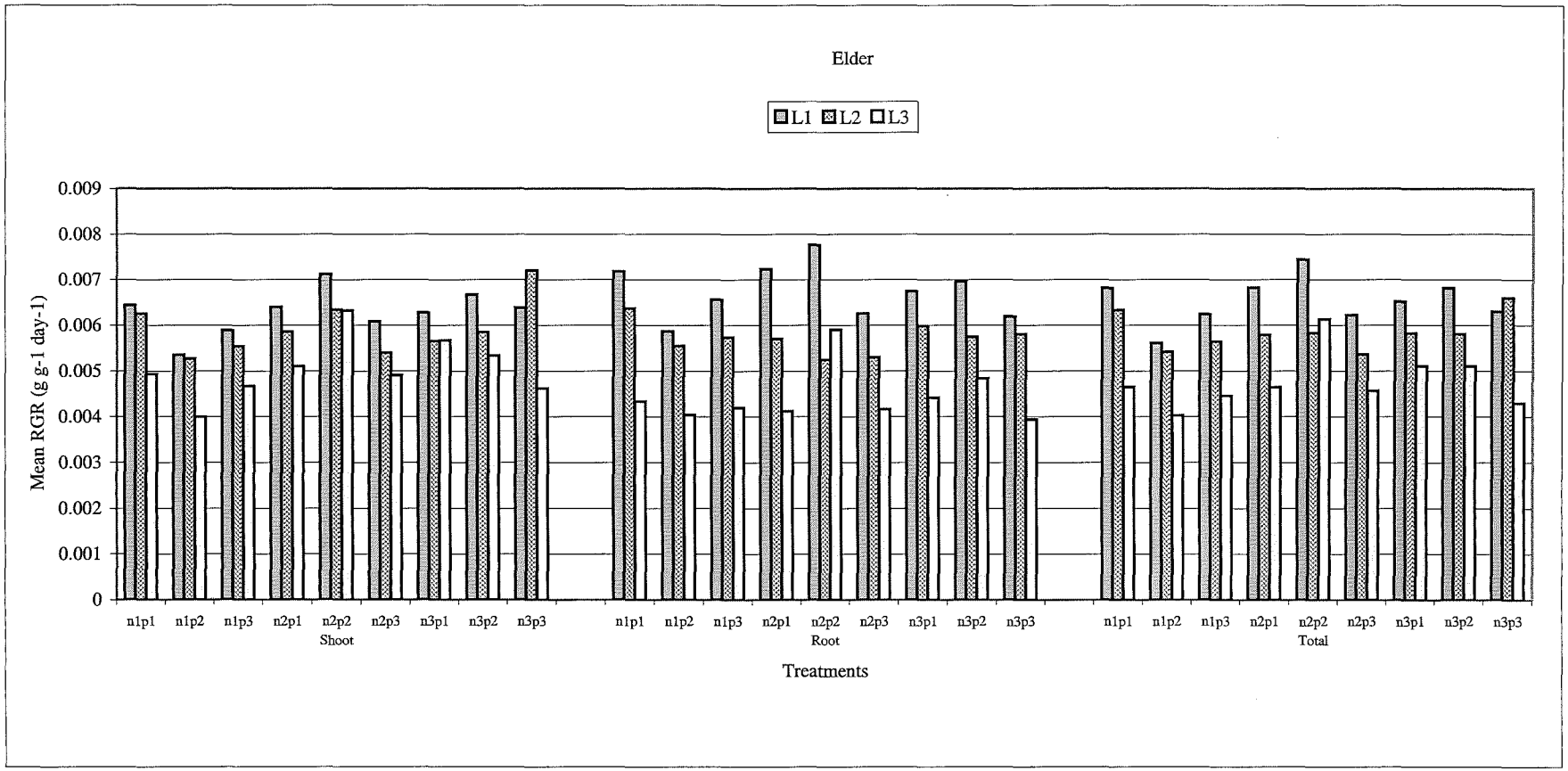


Figure 5.11: Mean relative growth rate of elder under different treatments

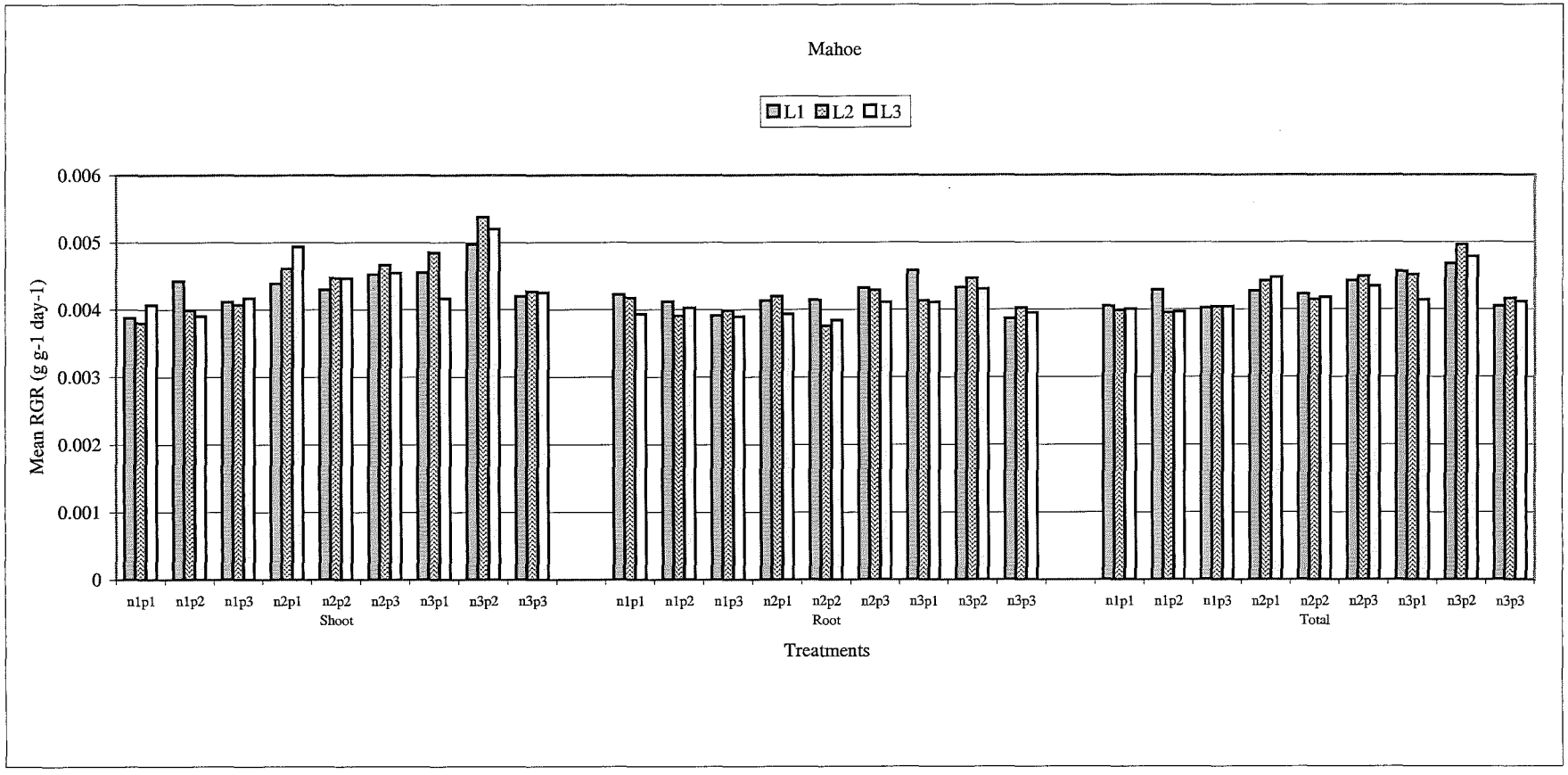


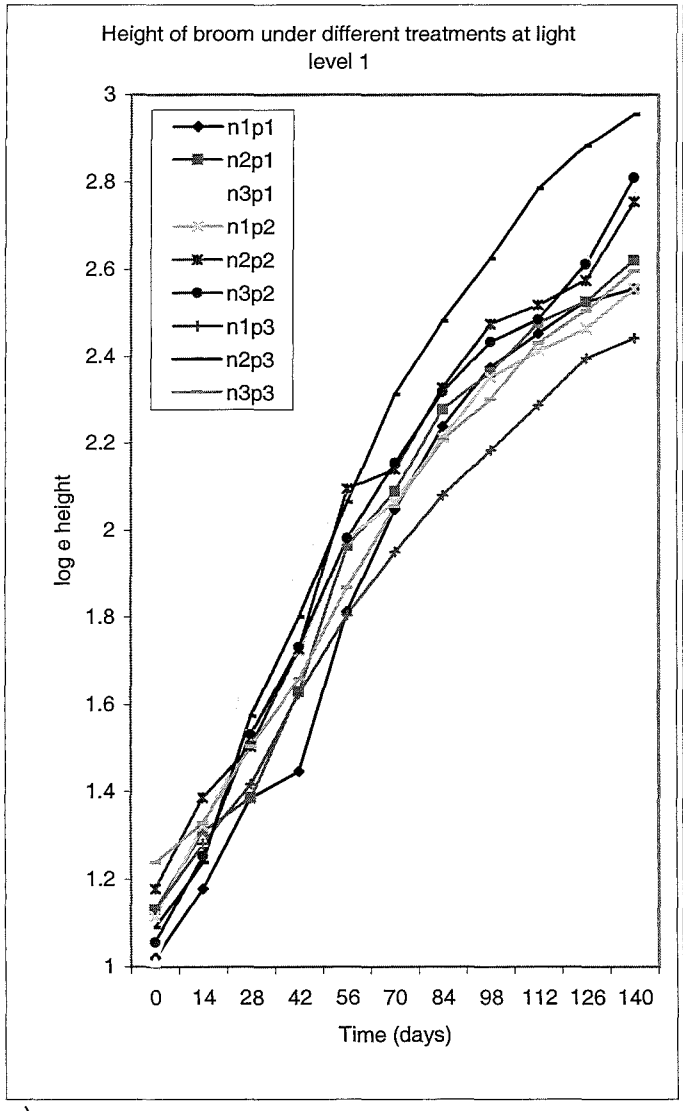
Figure 5.12: Mean relative growth rate of mahoe under different treatments

5.4.3.2.4. Height

The final height of broom was significantly affected by light ($F(2,81)=72.6$, $P\leq0.001$), N ($F(2,81)=8.3$, $P\leq0.01$), light*N ($F(4,81)=4.3$, $P\leq0.01$), N*P ($F(4,81)=3.4$, $P\leq0.05$) and light*N*P ($F(8,81)=2.6$, $P\leq0.05$) while P and light*P did not have significant effects. Broom height growth was highest at L1 followed by L2 and L3 (Figure 5.13). Both light and nitrogen level comparisons on broom revealed that height was significantly different between treatment levels 1&2 and 1& 3 (Tukey's test, $P\leq0.05$). Phosphorus had no significant effect on height growth of broom.

In the case of elder, there was a significant increase in height between light levels L1 & L3 (Tukey's test, $P\leq0.05$) (Figure 5.14). Different Phosphorus levels showed a significant increase in height between P levels P1 & P2 ($P\leq0.05$) while N levels showed no significant effect on height growth of elder.

For mahoe none of the light levels showed a significant effect, with mahoe able to grow to the same height irrespective of light (Figure 5.15). Height of mahoe was however, significantly affected by N ($F(2,81)=32.8$, $P\leq0.001$), P ($F(2,81)=30.5$, $P\leq0.001$) and N*P ($F(4,81)=4.7$, $P\leq0.01$) while the other treatments were non significant. Height growth of mahoe significantly increased ($F(2,81)=32.7$, $P\leq0.001$) with increasing N concentration. At treatment level significant differences showed between N1 & N2 and N1 & N3 (Tukey's test, $P\leq0.05$). Mahoe showed less height growth in P3 than P2 treatments. Height growth was significantly different between all P levels (Tukey's test, $P\leq0.05$).



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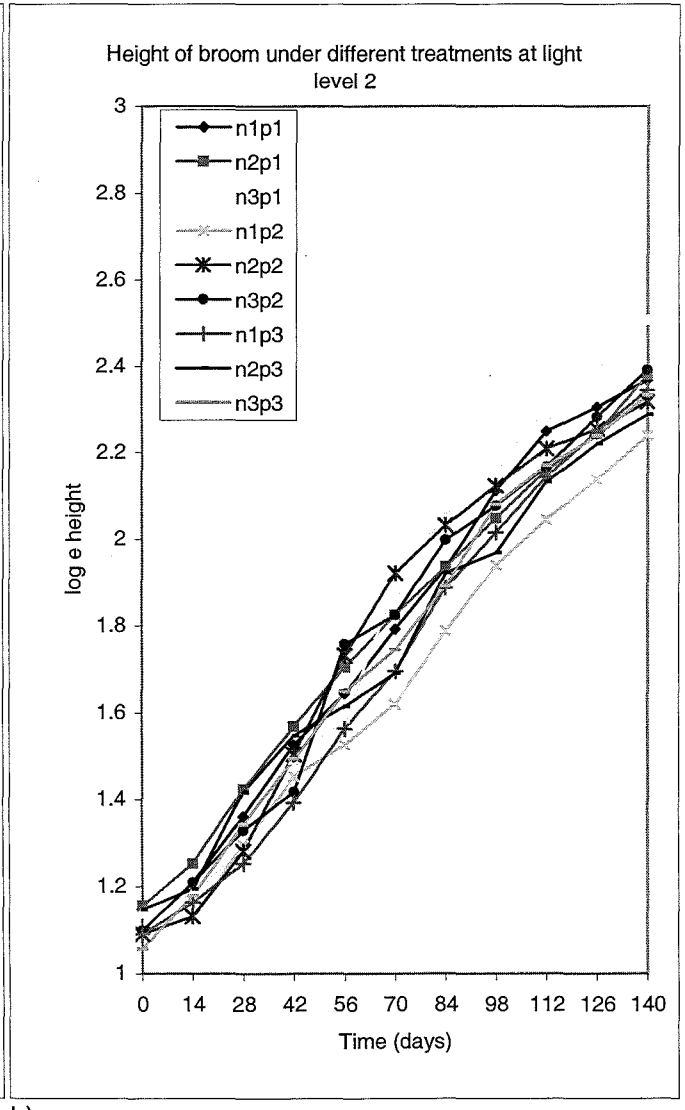

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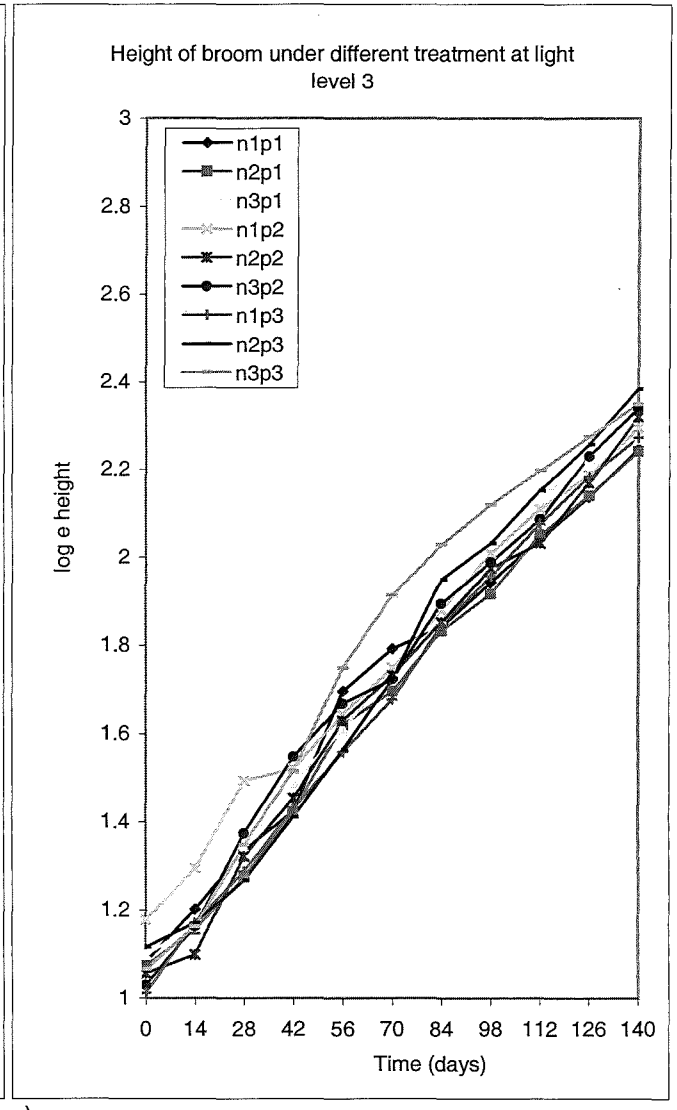

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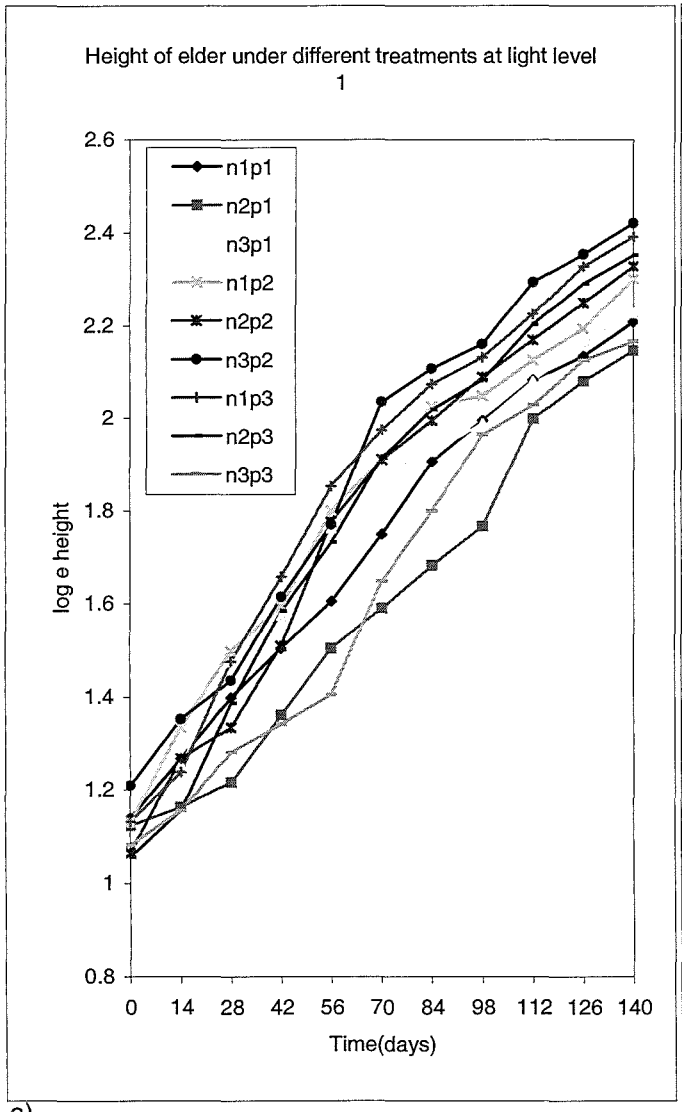
Figure. 5.13: Height of broom under different treatment according to light levels



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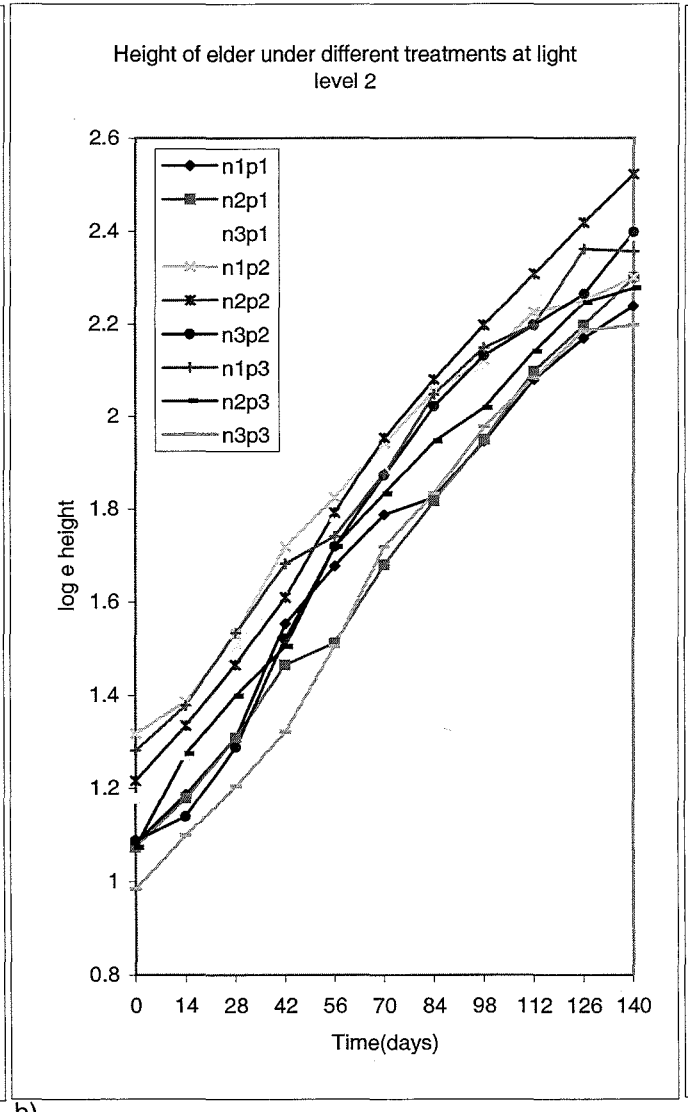

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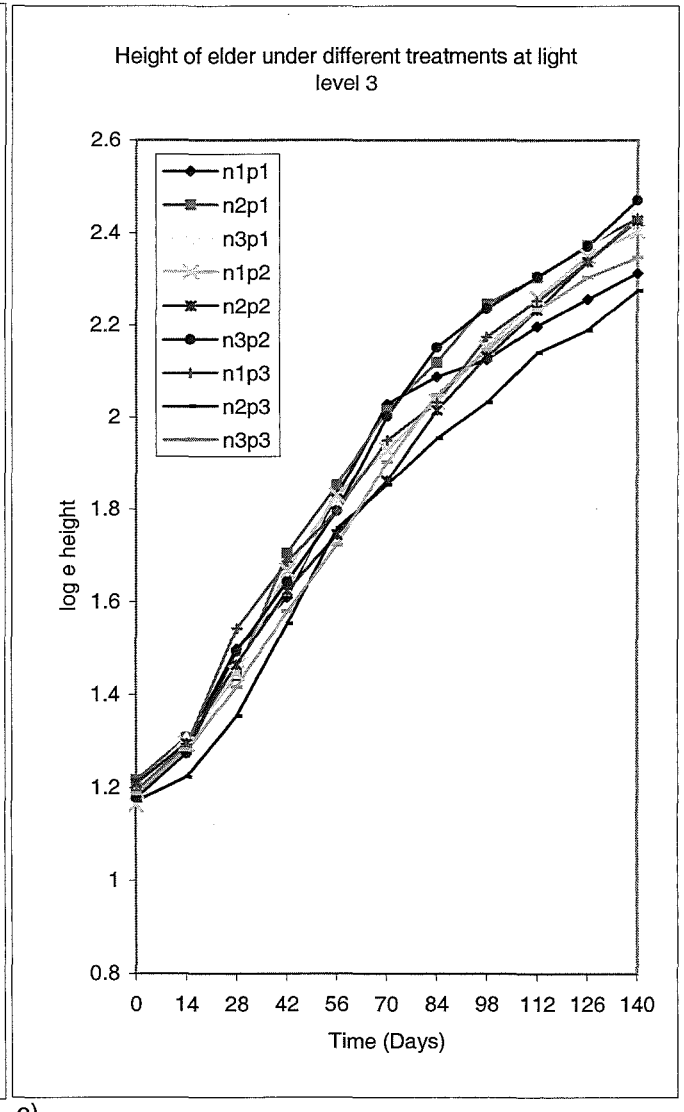

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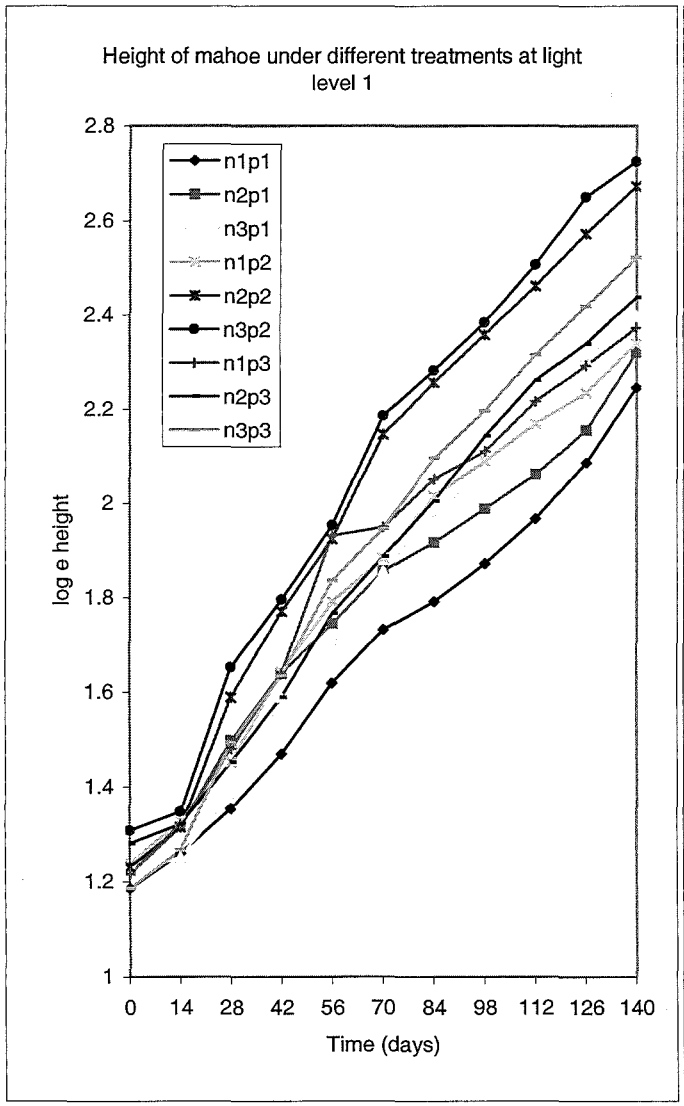
Figure. 5.14: Height of elder under different treatment according to light levels



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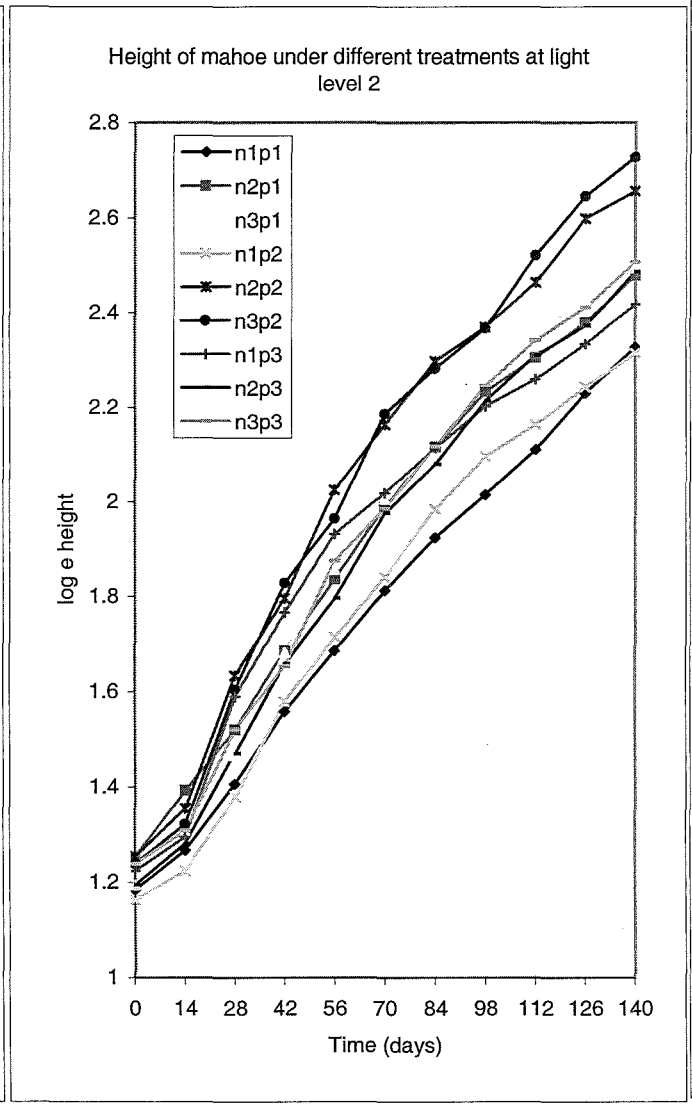

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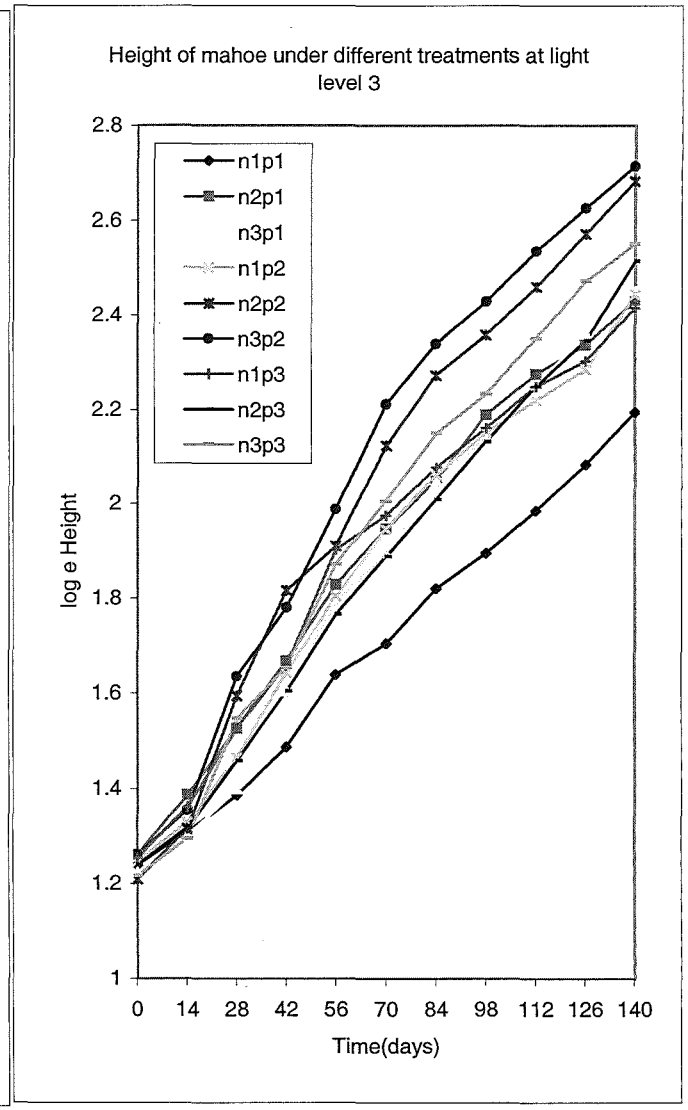


c)

Figure. 5.15: Height of mahoe under different treatment according to light levels

5.4.3.3. Discussion

Effect of light

After a disturbance (such as a tree fall gap or fire) the amount of light reaching the ground increases and nutrient levels generally remain the same as just before the disturbance. Light dependent growth of broom found in this study, fits well with a gap environment. Gradual disappearance of broom, as the vegetation becomes more dense may be explained by significantly reduced growth of broom seedlings under shaded conditions.

In Experiment 1, where only different light levels were tested, elder grew with out a significant effect from light. But in the second experiment elder showed a significant decrease in biomass (shoot, root, total) when light level decreased from L1 to L3 but the effect of light was not significant between L1 & L2. This dissimilarity may be a result of an interactive effect between light and nutrients that might well occur under natural environmental conditions. Both experiments also showed that elder growth was not significantly affected by light, up to the light level 2, indicating elder's ability to tolerate lower light conditions than broom (which significantly decreased its growth with increasing shade in every level). This also supports other studies which have reported that elder is intolerant of heavy shade (Tansley 1939, Roxbrugh 1992).

Mahoe's shade tolerance was evident in this experiment (as in the Experiment 1), with no significantly different effect from light and the fact that it performed best under L2 treatment, strengthening its position in the successional pathway under more shaded conditions. Even though shaded conditions are preferred, mahoe's ability to grow in well lighted conditions can be considered as a flexible adaptation. Harcombe (1977) suggested that it is advantageous for later successional species to be able to grow well in newly disturbed sites if they can arrive in such site.

Root /shoot ratio of broom and elder were significantly influenced by light with an increasing ratio with decreasing light. This result is contradictory to that found in the light only trial (Experiment 1) where root/shoot ratios decreased with increasing shade. Generally, a plant allocates comparatively more to the above ground biomass under more shaded conditions as an adaptation to increase photosynthetic tissues. Therefore, the increased R/S ratio could be a result of interactions between the different light and nutrient treatments. It is also possible that damage occurred to roots through overheating due to pot coverings, despite ventilation holes, which might have reduced the root/shoot ratio under high light levels. However, mahoe's root/shoot ratio was not significantly affected by light. That mahoe's resource allocation patterns were unaffected by different light levels also shows mahoe's tolerance of shade as changes in allocation patterns are a result of a plant's effort to overcome some sort of stress conditions.

Considering the effect of light in the two experiments, on the seedling growth of broom, elder, and mahoe the relative requirement of light decreases in the order of broom>elder>mahoe.

Nutrient effect

Broom biomass and growth rate were significantly affected by different P treatments by having more biomass and increased growth rate with increasing concentrations. Different levels of phosphorus did not have a significant effect on biomass, growth rate or biomass partitioning of elder and mahoe. Lack of growth responses (except height growth) by elder and mahoe to different levels of P may suggest an ability to tolerate low nutrient levels that can be experienced in the later successional stages where plants compete for limited nutrients.

Broom biomass (shoot and total biomass) and growth rate (RGR(shoot), RGR(total)) were significantly affected by different N treatments by having more biomass and increased growth rate with increasing concentration. N also significantly affected

biomass and growth rate of both elder (shoot biomass, RGR(shoot)) and mahoe (shoot and total biomass, RGR(shoot), RGR(total)). This means all three species have the ability to exploit higher N levels.

Unlike light, nutrient availability does not show a major increase after a disturbance in a secondary successional site such as tree fall gap. For broom seedlings to be successful in these sites, efficient use of available nutrients are needed as it is sensitive to reduce nitrogen levels. The nitrogen fixation ability of broom may also be a reason for its success.

The nutrient condition of the growing medium is known to affect biomass partitioning (Clarkson and Hanson 1980). Nitrogen is known to influence the growth of leaves (Ingestad and Lund 1979) thus affecting the root/shoot ratio. Unlike light, different nutrient concentrations did not have a significant effect on biomass partitioning of broom and elder which suggests comparatively less stress under different nutrients than different light levels. For mahoe, the root/shoot ratio was significantly affected, with an increased allocation to roots when N concentration decreased. This may be because, in a nutrient poor environment, low nutrient conditions increases the necessity to spread the root system to a greater area in order to gain as much nutrients as possible. The other possibility may be because N, being a component in chlorophyll is known to have a major effect in leaf production and under low N conditions the leaf biomass decreases resulting an increase in the ratio. A plant could increase its fitness under resource limiting conditions by increasing resource uptake, decreasing resource loss or increasing efficiency of conversion of internal stores to new growth (Chapin 1980). Mahoe's trend in increasing root/shoot ratio under low nutrient conditions can be seen as an attempt to increase uptake or conserve resources by limiting new growth.

Vitousek and Walker (1987) suggested nutrient availability to elevate in the middle of secondary succession as a result of early successional species returning nutrients to the soil by producing easily decomposable nitrogen rich litter. Therefore,

significantly affected growth of elder and mahoe by N may suggest that they dominate the vegetation at those periods where nutrient supply is still high and gradually disappear when nutrient demand exceeds the supply in the later stages of succession. In the view of the foregoing, the hypothesis that the relative dominance of broom, elder and mahoe in the successional sequence is controlled by their requirement of light and nutrients can not be rejected. Perhaps, establishment and survival stages in particular can be explained by their differences in light and nutrient requirements. It can also be suggested that the species order in the postulated successional sequence possibly represents an early to mid successional stages. Furthermore, Miller (1981) reported that nitrogen is more likely to be the limiting factor in the later stages of a secondary succession as both the vegetation and the forest floor are accumulating nutrients simultaneously. Therefore, elder and mahoe may not represent later successional stages as they showed greater ability to exploit N resources.

Interactive effects

Plants require several resources for successful growth and the total effect of resources depend on the relative importance of each resource at a specific time. Tilman (1980) categorized resources as 'perfectly substitutable', 'complementary', 'antagonistic', 'switching', 'perfectly essential', 'interactively essential', or 'semi essential'. The resources tested in this experiment are 'essential' and Tilman (1988) predicts an increase in one resource cannot overcome a limitation by another. Accordingly if a plant is limited by light, increase levels of P and N would not give an increase in growth rate provided resources are essential to the plant. Light, nitrogen and phosphorus are essential (although requirements are different between species) there were no significant interactive effects of resources on growth rate of any species. This means that the interactive effects of the resources did not change the outcome of the most limiting factor. However, there was a significant interactive effect of N*P in biomass of broom (total biomass), elder (shoot and total biomass) and mahoe (root, shoot and total biomass).

5.4.3.4. Conclusions

The following conclusions can be drawn as a result of the findings from the two experiments described in this chapter;

1. Broom seedlings are sensitive to changes in light levels with significant reductions in biomass production and growth rat at reduced light levels.

2. Elder grew most successfully under moderate light conditions and can tolerate light variations without significantly affecting its growth.

3. Mahoe seedlings are unaffected by light and able to grow significantly unaffected at lower light levels.

4. Considering the results of experiment 1 and 2 light sensitivity of the three species decreases in the order of broom>elder> mahoe.

5. Different levels of nitrogen proved significantly more important for the growth of mahoe than different levels of light. All three species were sensitive to different levels of N.

6. Broom was most sensitive to different levels of phosphorus as broom biomass and growth rate were significantly affected while biomass and growth rate of both elder and mahoe, were not significantly affected by different P levels (Tables 5.9 and 5.10).

Chapter 6

The water requirements of broom, elder and mahoe

6.1. Introduction

This chapter separately describes five experiments examining the water requirements of broom, elder and mahoe in relation to their successional positions. A general conclusion which emphasizes the potential influence of species specific water requirements in the successional sequence is provided.

Plants are dependent on water. Water is a constituent of protoplasm, often comprising up to 95% of the total plant weight. Water is essential to maintain carbohydrates, proteins and nucleic acids in a hydrated state (Sutcliffe 1979). Water is the medium for the movement of substances in the xylem and phloem, a medium for motile gametes to complete fertilization, and also an aid in the dissemination of spores, fruits and seeds (Sutcliffe 1979).

Water availability alone is the most significant factor determining the vegetation distribution patterns on earth (Kramer 1969). Limiting water supply has a much greater effect on the species composition of a forest than on the existence of the tree form (Crawford 1989). Therefore, water availability is an important environmental factor that influences the distribution and abundance of plant species in natural communities (Dias-Filho and Dawson 1995). Water limitations have a great influence on carbon assimilation and transpiration in a plant (Bradford and Hsiao 1982), affecting cell expansion and growth. Plant species show variable tolerance and physiological responses to water limiting conditions to conserve water loss and

to maintain positive turgor pressures (Jones *et al.* 1981; Dias-Filho and Dawson 1995).

A knowledge of plant resource acquisition patterns and tolerance to resource limitations is crucial for understanding community dynamics (especially succession) following disturbance (Evans and Ehleringer 1994), as species composition is generally considered to be a result of the competitive interactions at a site (Harper *et al.* 1961; Whittaker 1972). Differences in the competitive abilities of plants for resource acquisition of both invading and resident species determines the rate and composition of forest development during secondary succession (Van Hulst 1987).

During plant succession, varying degrees of water stress conditions arise. The species occurring at different stages of a succession are likely to have different types of tolerance mechanisms to deal with water stress. When water is limiting, plants with mechanisms to conserve and use water more efficiently may be more successful in colonizing dry conditions than those species accustomed to moist conditions (Turner and Jones 1980; Bradford and Hsiao 1982). Water stress is a very common environmental condition, and plant species more tolerant of these conditions, have a better chance of survival. Wieland and Bazzaz (1975) mentioned efficiency and depth of water use as one of the factors that influence the competitive displacement or co-existence of plants. The comparison of the responses of species from various successional stages, to determine their organization with respect to environmental gradients, is important in identifying successional sequences (Tilman 1988).

Drought has been suggested as a key factor in forest mortality and is thought to be partly responsible for the present vegetation pattern in New Zealand (Jane and Green 1986; Innes and Kelly 1992). Soil water deficits change considerably throughout the country, ranging from 0-400 mm per year on average (Coulter 1975). Summer droughts in the Canterbury region are common and occasional severe droughts also occur (e.g. the severe drought during 1987-1989, in which Canterbury received only 65% of normal rainfall (Innes and Kelly 1992)).

An examination of the water requirements of broom, elder and mahoe is expected to provide an understanding of their different responses, which may then be related to their successional positions. The experiments described in this chapter test the hypothesis that the order of species in the broom→elder→mahoe successional sequence is dependent on specific differences in their water requirements.

6.2. Experiments

Five separate experiments were conducted to examine the water requirements of broom, elder and mahoe.

1. The effect of water stress on seedling growth.

2. Plant relative water content under water stress conditions.

3. Root penetration under water stress conditions.

4. Seed germination under different soil water stress conditions

5. Water use efficiency.

6.3. Data analysis

Microsoft Excel 97 and SAS/STATS 6.12 SAS Institute (1995) were used for statistical analysis. Analysis of variance procedures, GLM procedures for unbalanced data, and regression analysis were performed, depending on the experimental design. When significant differences were observed between means, Tukey's test was used to determine the strength of the differences.

For derived variables in the seedling growth under water stress trial (Root/ Shoot ratio, Root weight ratio and Shoot weight ratio) SAS univariate procedure was used

to test normality. As the distribution was approximately normal, it was analyzed as for the other variables. Sokal & Rohlf (1981) reported some derived variables may not follow a normal distribution.

6.4. Experiment 1: Seedling growth under water stress

6.4.1. Introduction

Water availability controls plant growth more than any other environmental factor, with perhaps the exception of temperature (Sutcliffe 1979). The effect of water stress on plant growth is generally well recognised. In addition to maintaining a high turgor in plant cells, water is important for plants as a constituent, solvent, and a reactant (Kramer and Boyer 1995).

Droughts are common in natural environments and soil water status varies between sites. Topography, soil properties, climate and microclimate also influence soil water status in addition to precipitation. Disturbed or exposed sites may expect a different soil water status than sheltered sites, due to the increased evaporation from the soil surface. Diurnal and seasonal water stress conditions may well determine successful colonisation. Some species growing in these conditions show a capacity to withstand limited water resources. Experiment 1 characterises the growth responses of broom, elder and mahoe seedlings under soil water stress.

6.4.2. Materials and methods

6.4.2.1. Seedling preparation

The seeds of broom, elder and mahoe were raised in planting trays for 6 weeks. Initial sampling was undertaken by sorting seedlings according to their height and appearance as described in Section 5.4.3.1.1. Forty six seedlings from each species that fell in the middle of this range were selected for the experiment. These seedlings

were considered representative of height and appearance of the seedlings. Thirty of the chosen seedlings from each species were transplanted into 15 plastic pots (4 litre) containing nursery top soil compressed at an average bulk density of 1.3 g cm^{-3} (Method by Culley 1993). Each pot contained two seedlings and measurements for the two seedlings were averaged at the end of the experiment. The treatments began 4 weeks following transplanting into pots. After 4 weeks in the pots, the seedlings were divided into three groups (with each group containing 10 seedlings of each species). Each group was subjected to one of three soil moisture level treatments. An additional five seedlings from each species were randomly chosen to obtain initial dry weight. The remainder of the seedlings were subjected to the same treatments as the experiment and used as back-up samples.

6.4.2.2. Experimental design and treatments

The experiment involved a completely randomized design, with three soil moisture levels and three species with five replicates. Pots were randomly located on three glass-house benches and rearranged on a weekly basis throughout the experiment. Glass-house conditions consisted of a 16 hours light/8 hour dark regime and a temperature of $18/15^{0}C$. The experiment ran for 20 weeks.

The three soil moisture treatments used were field capacity (T1), stress level 1(T2) and stress level 2 (T3).

T1= Field capacity- the pots were watered regularly in order to keep the water content at the field capacity.

T2= Stress level 1- at the beginning of the experiment the seedlings were well watered to field capacity and then watered to field capacity every 10 days.

T3= Stress level 2 - watered to the field capacity at the beginning of the experiment and then watered to field capacity every 20 days.

The amount of watering differed according to the treatment. For instance, T2 required less water to reach field capacity after being left 10 days without watering, than the amount required by T3, left 20 days without watering. On the watering day for each treatment pots were kept on a stand and water was applied gradually at the top of the pot and also from the base of the pot through the holes at the bottom by putting water on to the collecting trays. Soil was carefully aerated during watering in order to allow maximum water intake. Initially, all the supplied water was absorbed by the soil and later on water started to collect on the trays. When water from the top of the pot drained through to the bottom of the pots it was assumed that the soil had reached field capacity and the pots were taken back to the bench.

The gravimetric water content of soil in each treatment was determined on every 20 th day, before re-watering throughout the experiment. Five randomly selected pots from each treatment were used at each time for the determination of soil water content. Five grams of soil from selected pots were obtained using a sampling tube and water content was measured by the oven dry method as described by Topp (1993). The soils taken from these pots to measure water content were replaced with the same amount of soil from back-up pots (see Section 6.4.2.1) that represented the same treatment. The water contents of the soil in the three treatments during the experiment are illustrated in Figure 6.1.

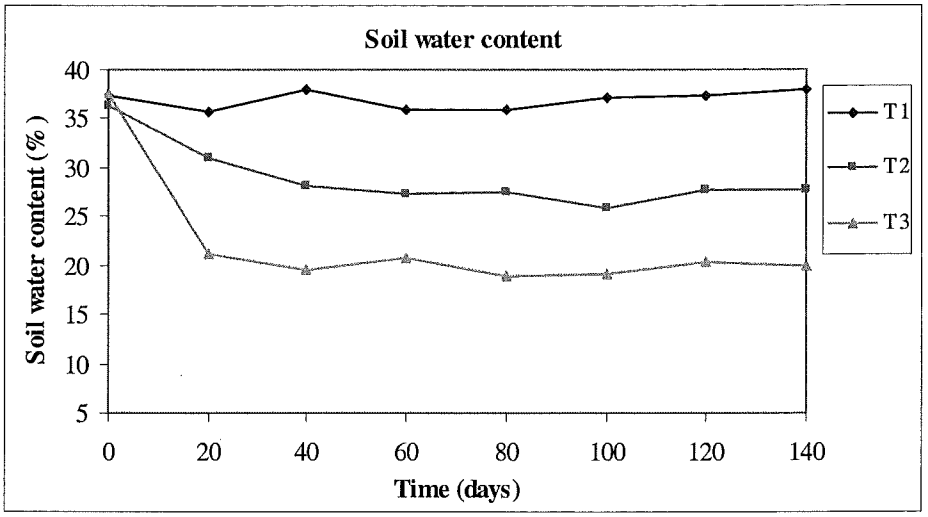


Figure 6.1. The mean gravimetric water content of the soil in different treatments during the experimental period.

6.4.2.3. Measurements and calculations

1. Five seedlings from each species were used to determine the initial dry weight. These seedlings were randomly chosen from the initially sampled seedlings. Initial dry weights of shoot and root portions were recorded.

2. The height of every seedling was recorded at the beginning of the experiment and fortnightly thereafter.

After the final recording of height at 20 weeks, all seedlings were harvested. Plants were carefully uprooted, washed and divided into root, shoot portions and then dried at $80C^0$ for 48 hours before determining dry weight.

Relative growth rate

Relative growth rate (RGR), the increase in plant mass per unit mass per unit time is commonly used to measure plant performance and was calculated for the total plant (RGR(total), root (RGR(root) and shoot (RGR(shoot) according to the Equation 6.1. (Hunt 1982).

$$RGR = \frac{\log_e M2 - \log_e M1}{t2 - t1} \quad \text{Equation (6.1)}$$

Where:

$\log_e M1$ is the natural logarithm of dry mass at time t1 and $\log_e m2$ is the natural logarithm of dry mass at time t2.

Root-shoot ratio, root-weight ratio and shoot-weight ratio

The calculation of biomass partitioning between different parts of a plant is useful to understand growth economy under different environmental conditions. Root-shoot ratio, root dry weight ratio (RWR), shoot dry weight ratio (SWR) were calculated to assess partitioning of biomass between root and shoot portions. Shoot and root dry weight ratios were calculated by dividing the dry weights of root or shoot by total dry weight. The relationship between RWR and SWR is:

$$RWR + SWR = 1 \quad \text{.....Equation (6.2)}$$

6.4.3. Results

6.4.3.1. Dry weight

Biomass production decreased with increasing water stress for all species (Figure 6.2). The percentage reduction in total biomass was marginally less in broom compared to elder and mahoe. The reduction in mean total dry weight of broom was

18% (in T2) and 26% (in T3) compared to T1. For elder, the reduction of total biomass was 30%(T2) and 42% (T3) while mahoe reduced by 23% (T2) and 34% (T3) compared to T1. Elder produced the highest total, shoot and root biomass in T1 (well-watered treatment).

Shoot and root biomass also followed a similar pattern to total biomass under water stress conditions. Elder suffered the most when water stress was increased to T3; with root biomass reduced by 41%, and shoot biomass by 43% compared to T1. For mahoe, the reduction of biomass in T3 was 31% (root) and 36% (shoot) compared to T1. The reduction of biomass in broom was comparatively less in T3; 22% (root) and 29% (shoot) compared to T1.

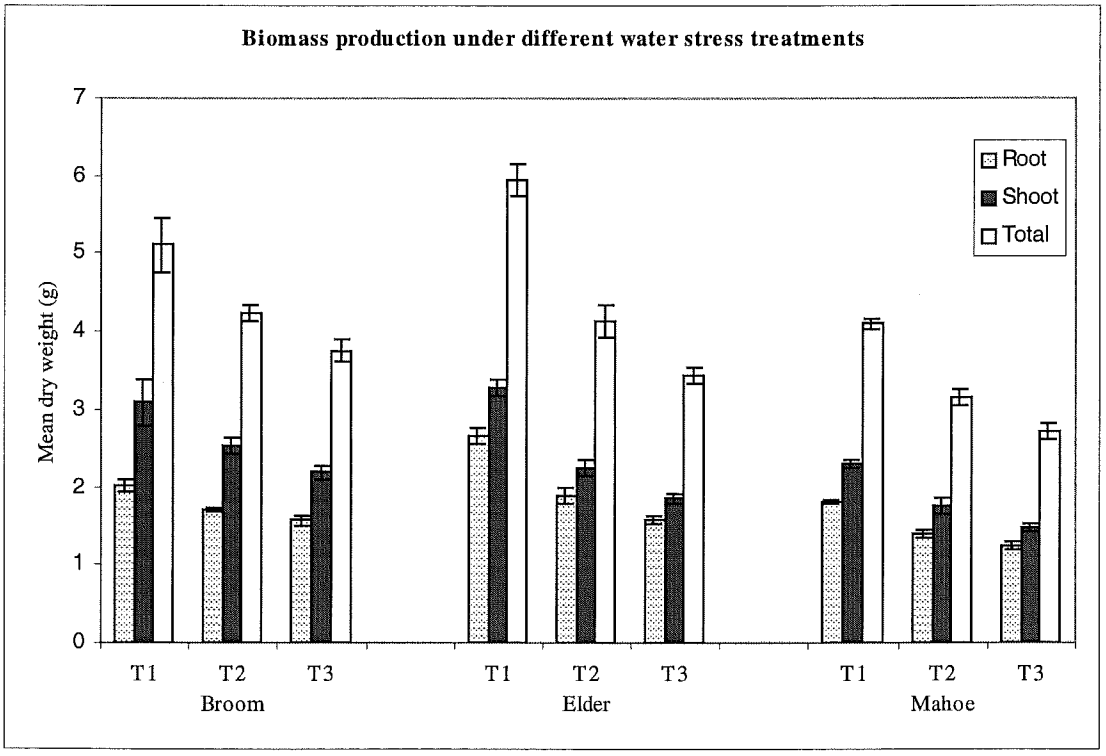


Figure 6.2. Biomass production of broom, elder and mahoe under different water stress treatments.

Initial analysis of main effects using SAS GLM procedures showed that there were significant differences in the dry weights of shoot, root and total plant between treatments and species (Table 6.1). Therefore, further analysis was used to determine the strength of effects at species and treatment level. The means compared at species level using Tukey's test showed that water stress treatments had a significant effect on the root dry weight of all species. The treatments also had a significantly different effect on shoot dry weight and total dry weight between elder and mahoe, and broom and mahoe. The differences between broom and elder were not significant (Table 6.2).

Table 6.1. Results of SAS GLM procedures showing main effects of variables on biomass production.

Variable	DF	Shoot		Root		Total	
		F value	P value	F value	P value	F value	P value
Species	2,36	12.9	0.001	15.3	0.001	17.3	0.001
Treatments	2,36	36.4	0.001	21.6	0.001	11.2	0.001
Species*treat	4,36	2.4	0.05	3.1	0.05	3.6	0.05

Table 6.2. Tukey's test results of species level comparison of root, shoot and total biomass of different species. (* indicates that the comparisons between species are significantly different (P≤ 0.05)).

Variable	Species comparison	Significance
Root biomass	B-E	*
	E-M	*
	M-B	*
Shoot biomass	B-E	n.s
	E-M	*
	M-B	*
Total biomass	B-E	n.s
	E-M	*
	M-B	*

Analysis at the treatment level (Tukey's test) showed broom root dry weight and shoot dry weight reduction with increasing water stress was significantly different (Tukey's test, P≤0.05) between T1 & T2 and T1 & T3, but not significant between T2 & T3 (Table 6.3). However, total biomass production in broom was significantly different between treatments. For elder there was a significantly different effect of water stress treatments between all variables (Tukey's test, P≤0.05) (shoot, root, total). The effect of treatments on biomass production (shoot, root and total) of mahoe were not significant between T2 and T3 while other comparisons were significantly different (Tukey's test, P≤0.05) (Table 6.3).

Table 6.3. Tukey's test results and means (± SE) of growth variables for seedlings of broom, elder and mahoe under three soil water stress treatments. (Means designated by the same letter are not significantly different (P≤0.05)).

Variable	Treatment	Dry Weight (g)		
		Broom	Elder	Mahoe
Root biomass	T1	2.01 ± 0.1 a	2.65 ± 0.11 a	1.79 ± 0.2 a
	T2	1.7 ± 0.02 b	1.88 ± 0.1 b	1.39±0.08 b
	T3	1.56 ± 0.06 b	1.57 ± 0.05 c	1.23± 0.05 b
Shoot biomass	T1	3.09 ± 0.15 a	3.28 ± 0.13 a	2.3 ±0.14 a
	T2	2.54 ± 0.1 b	2.25 ± 0.1 b	1.75 ±0.1 b
	T3	2.19 ± 0.09 b	1.85 ± 0.06 c	1.47±0.08 b
Total biomass	T1	5.1 ± 0.2 a	5.94 ± 0.2 a	4.1 ±0.25 a
	T2	4.2 ± 0.12 b	4.13 ± 0.21 b	3.14 ±0.16 b
	T3	3.75 ± 0.15 c	3.42 ± 0.1 c	2.7±0.14 b

6.4.3.2. Biomass partitioning

Root/shoot ratio showed an increase with increasing water stress in all species (Figure 6.3, Table 6.3). In broom R/S ratio increased by 10% (T2) and 15% (T3) compared to T1. Similarly the increase in R/S ratios in T2 and T3 treatments were 3% and 6% in elder and 6% and 10% in mahoe compared to T1 (Table 6.4). Elder had the highest R/S ratio but the percentage increase was the lowest compared to broom and mahoe. Statistical analysis showed that R/S ratio was significantly different ($F(2,36)=11.1$, $P\leq0.001$) only between species but the increase in R/S ratio was not statistically significant between treatments. At the species level, comparisons showed the R/S ratio was significantly different (Tukey's test, $P\leq0.05$) between broom and elder and mahoe and broom while the differences between elder and

mahoe were not significant. As R/S ratio was not significantly different between treatments further tests were not carried out.

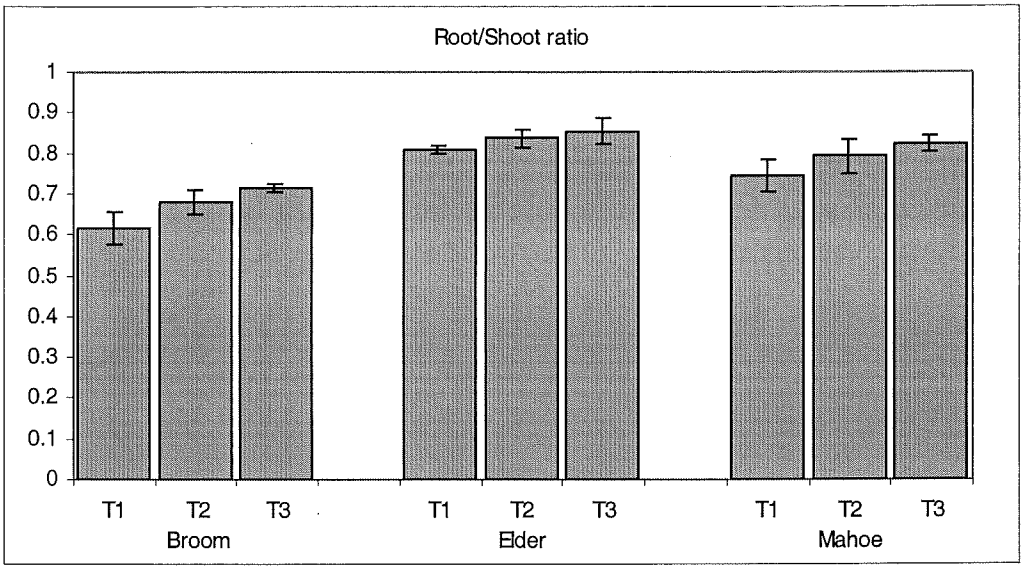


Figure 6.3. Root/ shoot ratio of broom elder and mahoe under different water stress

When comparing weight ratios, both RWR and SWR followed a similar pattern to R/S ratio. RWR and SWR were significantly different between species in response to water stress ($F(2,36)=11.7$, $P\leq0.001$). RWR showed an increase with increasing water stress, while SWR decreased (Figure 6.4); the effect of treatments on RWR and SWR was not significantly different. Species comparisons showed that both RWR and SWR were significantly different between broom and elder, and broom and mahoe (Tukey's test, $P\leq0.05$).

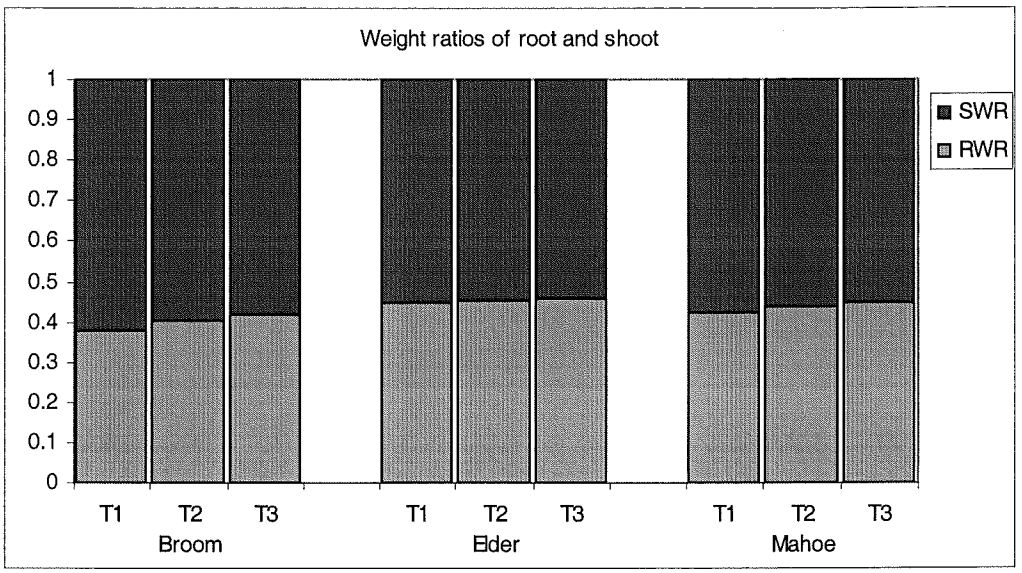


Figure 6.4. Weight ratios of shoot and root of broom, elder and mahoe under different water stress treatments.

Table 6.4. Biomass partioning of seedlings of broom, elder and mahoe under different water stress treatments (RWR=root weight ratio, SWR=shoot weight ration, R/S=root shoot ratio).

Treatment	Variables		
	RWR	SWR	R/S
Broom			
T1	0.3781	0.6218	0.6175
T2	0.4033	0.5966	0.6804
T3	0.4163	0.5836	0.7147
Elder			
T1	0.4462	0.5537	0.8068
T2	0.4543	0.5456	0.8349
T3	0.4593	0.5406	0.8544
Mahoe			
T1	0.4230	0.5769	0.7456
T2	0.4387	0.5612	0.7910
T3	0.4498	0.5501	0.8206

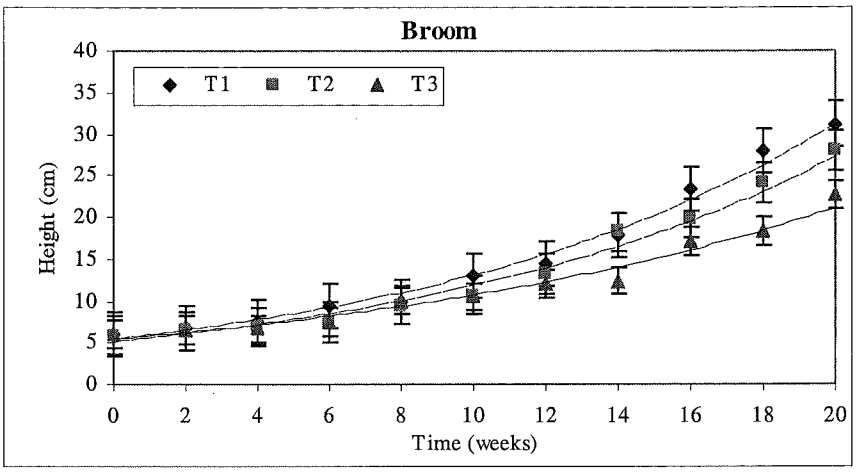
6.4.3.3. Height

Seedling height was significantly different (P≤0.001) between species (F(2,36)=45.9) and treatments (F(2,36)=73.1). Broom seedling height decreased by 10% (T2) and 27% (T3) compared to T1. The reduction in height growth of elder was 2% (T2) and 30% (T3) compared to T1 (Table 6.5, Figure 6.5 a, b). Height differences between T1 and T2 were not statistically significant for either broom or elder, while other treatment comparisons were significantly different. Seedling height of mahoe was significantly different between all treatments and showed 46% reduction in height growth in T3 compared to T1 (Table 6.5, Figure 6.5 c). Table 6.5 presents results of the Tukey's analysis of final seedling height. Regular height measurements were used to show changes in height during the experiment and are presented in figure 6.5 (a,b,c).

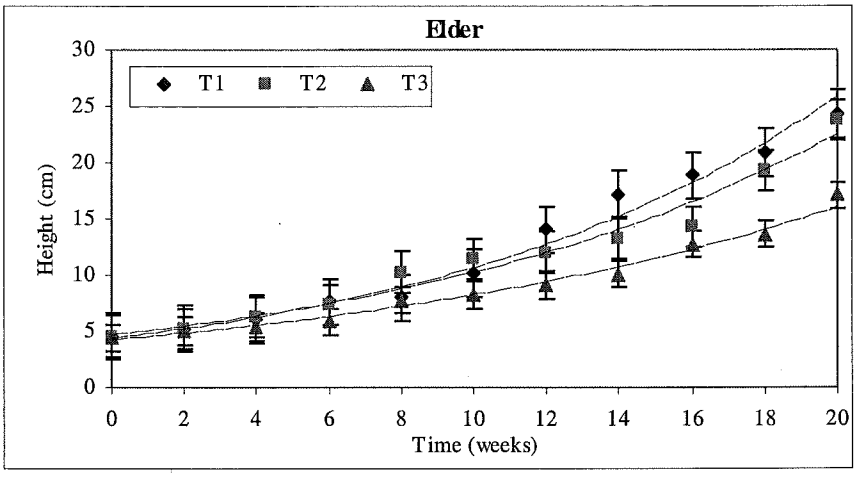
Table 6.5. Results of Tukey's test on mean final height reading (± SE). (Same letter represents no significant difference between treatments (P≤0.05) for respective species and each reading represents mean of 5 replicates).

Species	Treatment 1	Treatment 2	Treatment 3
Broom	31.2 ± 1.1 a	27.9 ± 0.7 a	22.7 ± 0.8 b
Elder	24.3 ± 0.5 a	23.8 ± 0.6 a	17.0 ± 0.8 b
Mahoe	26.7 ± 0.8 a	19.5 ± 1 b	14.4 ± 0.6 c

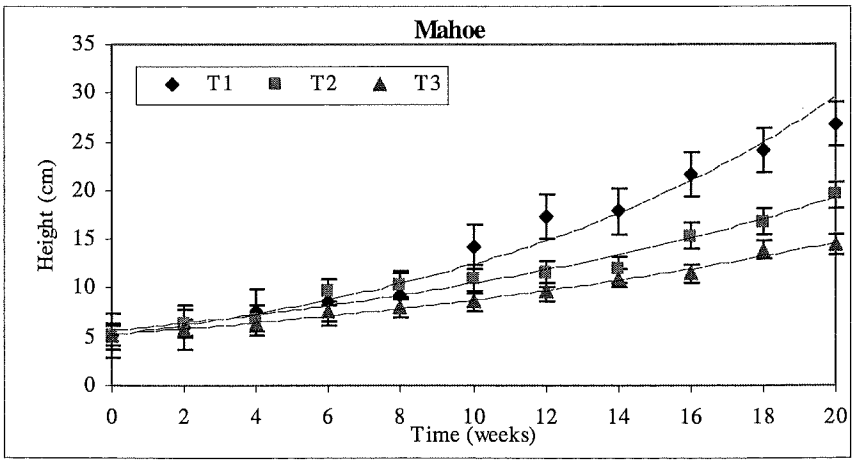
a)



b)



c)



Figures 6.5. Height growth of a) broom b) elder and c) mahoe under different water stress treatments.

A regression analysis was conducted to determine the nature of the relationship between seedling height and time in different species and treatments. In broom, the slope (b) of the function of height for both T1 and T2 was steeper than T3. (Table 6.6). For elder, the slope of the function of height growth decreased with increasing water stress while in mahoe, the decrease was steep from 1.13 in T1 to 0.65 in T2 and 0.46 in T3 (Table 6.6).

Table 6.6. Regression analysis of height against time showing estimates of intercepts (a) and slopes (b). (Figures shown are means ± SE).

Function parameters	Treatment 1	Treatment 2	Treatment 3
Broom			
A	2.47 ± 0.7	2.51 ± 0.62	3.877 ± 0.478
B	1.276 ±0.061	1.11 ±0.053	0.7919 ±0.040
r^2	0.88	0.89	0.87
Elder			
A	2.21± 0.43	2.95± 0.51	3.12±0.37
B	1.02 ±0.036	0.86± 0.043	0.589± 0.032
r^2	0.93	0.88	0.86
Mahoe			
A	3.04±0.42	4.75±0.42	4.62± 0.21
B	1.132 ±0.036	0.65± 0.035	0.463± 0.01
r^2	0.94	0.86	0.92

6.4.3.4. Growth rate

Water stress reduced RGR(total), RGR (root), RGR(shoot) in each of the three species (Table 6.8). Broom RGR(shoot) reduced by 13% (T2) and 23% (T3) compared to T1. Similarly, RGR(root) and RGR(total) of broom were reduced by 11% and by 13% in T2 treatment and by 18 % and 21% in T3 treatment, compared to T1.

Elder RGR(shoot) decreased by 26% (T2) and by 38% (T3) compared to T1. RGR (root) and RGR (total) of elder reduced by 23% and 25% in T2 and by 28% and 37% respectively in T3 compared to T1. Mahoe RGR(shoot) decreased by 16% (T2) and 26% (T3) compared to T1. RGR (root) of mahoe was reduced by 16% and by 23% in T2 and T3 compared to T1. RGR (total) reduction was 16% (T2) and 26% (T3) compared to T1.

Statistical analysis showed that the treatments had a significantly different ($P \leq 0.001$) effect on RGR(shoot), RGR(root), and RGR(total), ($F(2,36)=59.3$, 33.9, 65.8 respectively). Species also had a significantly different ($P \leq 0.001$) effect on RGR(shoot) and RGR(total) ($F(2,36)=26.1$, 15.7 respectively) while RGR(root) was significant at $P \leq 0.05$ ($F(2,36)=3.1$). At treatment level the reduction in both RGR(shoot) and RGR(total) were significantly different between T1 &T2 (Tukey's test, $P \leq 0.05$) but the differences were not significant between T2 & T3 (Table 6.8). Reduction in RGR(root) of broom was not significant between T1 & T2 while there was significant reduction between T2 & T3 (Tukey's test, $P \leq 0.05$). All growth rate parameters of elder were significantly reduced with increasing water stress (Tukey's test, $P \leq 0.05$) (Table 6.8). In the case of mahoe, reduction in RGR(root) was not significant between T1 & T2 while T1 & T3, T2 & T3 were significant (Tukey's test, $P \leq 0.05$). Both RGR(shoot) and RGR(total) of mahoe were significantly reduced (Tukey's test, $P \leq 0.05$) when water stress increased from T1 to T2 but the reduction in growth rate was not significant when water stress further increased from T2 to T3.

Table 6.7. Species level comparison of different variables. (* indicates the comparisons were significant at $P \leq 0.05$, Tukey's test).

Comparison	RGR(root)	RGR(shoot)	RGR(total)
Broom-Elder	n.s	n.s	n.s
Elder-Mahoe	n.s	*	*
Mahoe-Broom	n.s	*	n.s

Table 6.8. Treatment effect on growth variables of broom, elder and mahoe. (Means designated by the same letter are not significantly different at P≤0.05 (Tukey's test) for each treatment and each species).

Treatments	RGR(root)	RGR(shoot)	RGR(total)
	Mg g^{-1} day^{-1}		
Broom			
T1	9.54 ± 0.5 a	10.3 ± 0.4 a	10.05 ± 0.3 a
T2	8.46 ± 0.1 a	8.93± 0.3 b	8.75± 0.2 b
T3	7.79 ± 0.3 b	7.87 ± 0.3 b	7.84± 0.3 b
Elder			
T1	10.91 ± 0.3 a	10.27 ± 0.3 a	10.55 ± 0.3 a
T2	8.41 ± 0.24 b	7.54 ± 0.3 b	7.92 ± 0.4 b
T3	7.81± 0.3 c	6.19± 0.2 c	6.65 ± 0.2 c
Mahoe			
T1	10.79 ± 0.6 a	11.85 ± 0.4 a	11.44 ± 0.4 a
T2	9.10 ± 0.4 a	9.92 ± 0.4 b	9.59 ± 0.4 b
T3	8.28 ± 0.3 b	8.70 ± 0.4 b	8.51 ± 0.4 b

6.4.4. Discussion

Experiment 1 examined seedling growth under water limiting conditions. The results showed that soil water stress reduced growth (in terms of biomass, height and growth rate) and also affected the biomass partitioning of broom, elder and mahoe. The degree of sensitivity to water stress varied between species and also among different parts of a plant.

Amongst biomass variables, shoot biomass was most affected by water stress with maximum reductions in dry weight. Broom shoot biomass was reduced by 29% in T3 compared to T1, while elder and mahoe experienced greater reductions of 43% and 36% respectively. Kozlowski *et al.* (1991) reported seedling shoot growth was very sensitive to water stress. However, among the species tested in this experiment,

broom appears to have a better tolerance of water stress than the other species. Root dry weight also followed a similar trend to shoot dry weight, with reductions of 22% for broom, 41% for elder and 31% for mahoe in the severe stress treatment (T3) compared to T1. Root growth is also known to be reduced by increasing water stress (Kaufmann 1968; Kramer and Boyer 1995). Waring and Schlesinger (1985) also found poor growth in tree roots when soil water potential fell below –0.7 Mpa. Reduction in root dry matter production was maximum in elder and there were significant differences between each water stress level. The decrease in root biomass production followed a similar pattern in broom and mahoe with the exception of a relatively less percentage reduction in broom compared with mahoe (Table 6.3).

As shown in Figures 6.3 and 6.4, biomass partitioning was affected by soil water stress; root/shoot ratio and RWR increased with increasing soil water stress although the differences were not statistically significant between treatments. An increase in root/shoot ratio has been found in many species in response to increasing water stress (Fitter and Hay 1981; Kramer 1983; Nguyen and Lamant 1989; Wang *et al.* 1988). In general, plants appear to invest more of their resources into root production under stressful conditions although the role of root/shoot ratio in water stress tolerance is uncertain (Fitter and Hay 1981; Kramer 1983). Plants in drying conditions continue to grow roots while decreasing the growth of shoots (Kramer and Boyer 1995; Bennett and Doss 1960). Broom was shown a trend to allocate more biomass to roots under water stress (increase of R/S ratio, 10% in T2 and 15% in T3 compared to T1) although the increment was not statistically significant.

Relative growth rate variables also showed similar trends to dry matter production. Elder was most vulnerable to water stress, having the lowest root, shoot and total plant growth. The results of this study imply that the three species tested had differences in their ability to tolerate water stress. During the experimental period, elder showed most susceptibility to water stress with a reduction in all growth variables (except height). The effect of water stress on height growth followed a decreasing order broom>elder>mahoe. Broom was the most tolerant species to water stress in terms of growth rate, biomass and height. Bannister (1986) also reported that broom was able to grow without signs of stress under low soil water status. The

water stress tolerance of the three species at the seedling stage appears to increase in the order of elder<mahoe<broom.

6.5. Experiment 2: The determination of plant relative water content under different stress levels

6.5.1. Introduction

The water status of a plant can be expressed either by water content or water potential (Bannister 1986). Water potential is based on energy levels, while water content is based on the quantity of water in the plant tissue. Both water content and water potential have been used to describe the water status of plants although some suggest water potential fails to explain physiological responses despite its wide use (Hsiao 1973; Oertli 1976). There are limitations to expressing water status in terms of water potential and an approach based on cell volume (relative water content) could be more meaningful (Ludlow 1987; Sinclair and Ludlow 1985). Relative water content (RWC) is a useful indicator of the state of a plant's water balance as it expresses the absolute amount of water the plant requires to reach full saturation and can be measured more easily than water potential (Lamont 1999). Sinclair and Ludlow (1985) suggested relative water content was an important and possibly major determinant of metabolic activity and leaf survival and is also a fairly stable independent variable.

Relative water content is expressed as the percent water content at a given time as related to the water content at full saturation (Slavik 1974) and is often measured using leaves. RWC is expressed by the following equation (Catsky 1974) and was used in the present experiment.

$$RWC = \frac{\text{(Initial weight-dry weight)}}{\text{(Saturated weight-dry weight)}} \times 100 \quad \text{.....Equation. (6.2)}$$

6.5.2. Materials and methods

Seedling preparation, sampling method, soil, experimental design and glass-house conditions for the Experiment 2 were same as for Experiment 1 (Section 6.4.2.1).Two modifications were made; Seedlings were raised for a further 6 weeks prior to starting treatments in order to obtain sufficient leaves; also each pot contained only one seedling. Fifteen seedlings from each species were sampled and divided into three groups. Each group was given one of three water stress treatments.

6.5.2.1. Treatments

1) T1: Well-watered, where seedlings were watered to field capacity.

2) T2: Medium stress, where seedlings were watered to field capacity then left until the first sign of wilting occurred, then re-watered to field capacity. This procedure was repeated throughout the experimental period.

3) T3: Severe stress, where seedlings were watered to field capacity, then not watered again. Seedlings were observed each morning to see whether they recovered from the water stress and harvested when they showed no recovery from wilting for three days.

The top surface of each pot was covered in order to reduce evaporation. The experiment terminated at different times according to the treatments; well-watered and medium stress treatments ran for 6 and 12 weeks respectively, severe stress treatment terminated when seedlings did not recover from the water stress for three days.

6.5.2.2. Measurements

The measurements recorded were

1) time taken to first sign of wilting;

2) gravimetric soil water content at field capacity, first sign of wilting and permanent wilting; (method Topps (1993); soil taken from pots were replaced by the soil taken from the back-up pots relevant to the treatment and species as described in Experiment 1 (Section 6.4.2.2).

3) leaf relative water contents of species in each treatment.

6.5.2.3. Procedure for RWC determination

To determine the relative water content, the fresh weight of the experimental tissue is measured before and after saturation with water. A number of techniques have been used to reduce errors in sampling, water loss evaporation, and achieving saturation. The procedure followed here is modified from Bannister (1986) and Catsky (1974).

In treatment 1, five mature leaves from each plant were obtained. In treatment 2, five mature leaves were obtained from each plant at the first sign of wilting. In treatment 3, five mature leaves were taken when plants were fully wilted. The leaves obtained from each plant were placed in a sealed polythene bag and initial weights were recorded. This procedure was repeated 3 times for each plant during the experimental period.

Leaves in each sample were cut in half to enable a greater uptake of water and then placed between two layers of foam and stapled together lightly. Each sample was arranged in separate foam layers, lowered into a water bath and soaked for 24 hours to saturation. Saturated leaf sample weights were determined after leaves were surface dried on a series of filter papers. Samples were then dried in an oven at 80-

85^0C for 48 hours and re-weighed. RWC was then calculated according to Equation 6.2.

6.5.3. Results

All plant species maintained between 84 -88% relative water content in the well-watered treatment. With increasing water stress, RWC of all species significantly decreased (Table 6.9). Broom had the lowest (26.5) RWC (in treatment 3) at the time of experiment termination, indicating its ability to survive until RWC is quite low. For elder and mahoe, the RWC at the termination of the experiment in treatment 3 were 28.2 and 30.2 respectively (Table 6.10). Broom was able to delay the first signs of wilting until soil water content decreased to a level of 19.5 % (Table 6.10). Elder showed the first sign of wilting after 22.1 days when soil water content reached 20.9%. The first sign of wilting in mahoe occurred after 18.5 days, at 21.9% soil water content. Time taken to first sign of wilting and permanent wilting decreased in the order of broom>elder> mahoe.

SAS ANOVA revealed that time taken to both first sign of wilting and permanent wilting were significantly different between species ($F(2,42)=85.4$, $P\leq0.001$). Further analysis using Tukey's test showed time taken to first sign of wilting and time to permanent wilting were different between all species (Table 6.10).

Table 6.9. Mean relative water contents of broom, elder and mahoe in different treatments. (Results of Tukey's test to compare treatment effect: values designated with same letter in each column are not significantly different a $P\leq0.05$).

Treatments	RWC		
	Broom	Elder	Mahoe
T1	86.3±1.9 a	84.6±1.6 a	88.7±0.98 a
T2	54.4±3.0 b	61.3±1.1 b	63.5±1.6 b
T3	26.5±1.6 c	28.2±1.2 c	30.2±0.9 c

Table 6.10 Time (days) taken to the first sign of wilting and permanent wilting and soil water contents of broom, elder and mahoe. (Tukey's test results: values designated with same letter in each column are not significantly different at P≤0.05).

Species	Time (days) to first sign of wilting	Soil water content at first sign of wilting	Time (days) to permanent wilting	Soil water content at permanent wilting
Broom	23.6±0.30 a	19.5±0.43 a	34.5±0.97 a	16.9±0.35 a
Elder	22.1±0.29 b	20.9±0.33 b	31.2±1.1 b	17.3±0.26 a
Mahoe	18.5±0.25 c	21.9±0.35 b	26.5±0.92 c	17.5±0.46 a

6.5.4. Discussion

Plants which are able to adjust osmotically tend to have a high tolerance to drought as they are able to maintain turgor and avoid desiccation. Drought tolerant plants usually have a lower RWC at first sign of wilting (turgor loss point) than drought sensitive or drought-avoiding plants (Lamont 1999). Broom, elder and mahoe are significantly different in their leaf relative water content both at the first sign of wilting and at the permanent wilting. As a result these species vary in the ability to withstand water stress. Broom began wilting at a soil water content of 19.5% and survived until RWC of leaves decreased to 26.5%; consequently broom may be more suitable for open habitats where soil tends to dry quickly. Similarly both elder and mahoe started wilting at a soil water content of 20.9% and 21.9% and took significantly fewer number of days to wilt than broom. Wilting, in comparatively less time, when other factors are similar, also indicates higher transpiration of mahoe and elder compared to broom. Therefore both elder and mahoe may prefer sites that have less fluctuations in both evaporation from soil surface and transpiration from plant surface. These results are in agreement with Bannister (1986) who reported broom tolerated low leaf water potentials without showing signs of wilting; mahoe was shown to be a drought-susceptible species that wilted at relatively higher leaf water potentials.

6.6. Experiment 3: Root penetration and distribution under different levels of water stress

6.6.1. Introduction

Water is one of the many factors (e.g. soil texture, aeration, temperature, pH, presence of micro-organisms etc.) that can greatly affect root growth (Kramer and Boyer 1995). The distribution of water varies enormously between soils of different habitats (Reader *et al.* 1993) and water deficiency in soil is known to cause a reduction or cessation of root growth (Kramer and Boyer 1995). However, differences in rooting habitats and depths have been identified as a means of sharing soil resources, such as water (Hellmers *et al.* 1955; Wieland and Bazzaz 1975). Access to moisture in relatively deeper soil levels is therefore an important determinant of survival, especially at the seedling stage. It is possible that species have characteristics which are selected for fluctuating environments. In some species, the vertical extent of rooting increases during dry periods (Molyneux and Davies 1983; Sharp and Davies 1985). An examination of the rooting habits of broom, elder and mahoe under water limiting conditions, would provide information on their adaptive features which favor water acquisition. This information can then be used to relate to their successional positions.

6.6.2. Materials and methods

This experiment was designed to measure rooting depth in well watered and in un-watered conditions to determine the responses of broom, elder and mahoe roots. The trial was set up as a 3 species, 2 treatments, 5 replicates factorial design (3 x 2 x 5).

Seeds were germinated in petri-dishes on moist filter paper. Germinated seeds were raised in planting trays until they were 3-4 cm in height (approximately 4 weeks old). They were then transplanted into soil columns; each column contained one seedling. Soil columns were made using black polythene and each column was 1m deep and

10cm in diameter. The soil columns were supported by bricks placed in between them. Columns were filled with sieved potting mix with a composition of 33% of each of the following particle sizes: 4-2 mm, 2-0.8 mm and >0.8mm. Soil was packed to approximately 1.3 cm^3 bulk density in columns and watered to saturation. Excess water was allowed to drain through holes at the bottom of the columns. Seedlings were allowed to establish in the soil columns for 2 weeks with a regular water supply at or near field capacity before commencing treatments. The treatments were as follows:

1) Watered, where columns were watered with 50 ml per day;

2) Un-watered, where columns were not watered until the termination of the experiment after 3 weeks.

This experiment was conducted under glass-house conditions and the conditions were similar to Experiment 1 (Section 6.4.2.2.) The top surface of each polythene bag was covered in order to reduce evaporation.

6.6.2.1. Measurements

The following measurements were taken:

1). Shoot mass: At the termination of the experiment, the shoot dry weight of each seedling was measured.

2). Maximum rooting depth: After the shoot portion of each seedling was removed at the termination of the experiment, soil columns were cut into 10cm lengths. Soil was washed away to recover roots by submerging each cut section in water. Maximum root penetration was calculated by measuring the length of the longest root portions in each section and the values were summed.

3). Vertical distribution of root biomass: Dry weights of all recovered roots from each column section were determined.

6.6.3. Results

Broom roots penetrated the greatest depth followed by elder and mahoe (Table 6.11). Neither elder nor mahoe roots were found at the 30-40 cm level.

Analysis of variance procedures showed the maximum root penetration was significantly different between species ($F(2,24)=63.7$, $P\leq0.001$). At species level root penetration was significantly different between all species (Tukey's test, $P\leq0.05$). In a comparison of treatments effect, broom roots penetrated significantly deeper (Tukey's test, $P\leq0.05$) in the un-watered treatment than the watered treatment. In contrast both elder and mahoe root penetration was less in un-watered treatment. The decrease in root penetration in un-watered mahoe was significantly different (Tukey's test, $P\leq0.05$) while the decrease in elder root penetration was not significant (Table 6.11).

Figure 6.6 illustrates the relationship of mean maximum rooting depth between treatments. The dotted line in Figure 6.6 shows the hypothetical line for a 1:1 relationship between the treatments if there is no effect. Broom positioned over this line of the 1:1 relationship showing more length growth in the un-watered treatment while elder and mahoe positioned below the line due to less rooting depth in the un-watered treatment.

Table 6.11. Maximum rooting depths of broom, elder and mahoe in watered and un-watered treatments. (Mean values are presented ± SE. The same letter indicates that the comparisons between treatments and species are not significantly different (P≤0.05)).

Species	Watered treatment		Un-watered treatment	
	Maximum rooting depth (cm)	Mean maximum rooting depth (cm)	Maximum rooting depth (cm)	Mean maximum rooting depth (cm)
Broom	33.0	25.7±0.7 a	34.5	27.8±0.6 d
Elder	25.8	22.7±0.5 b	25.8	21.9±0.4 b
Mahoe	19.7	16.2±0.3 c	18.0	15.3±0.3 e

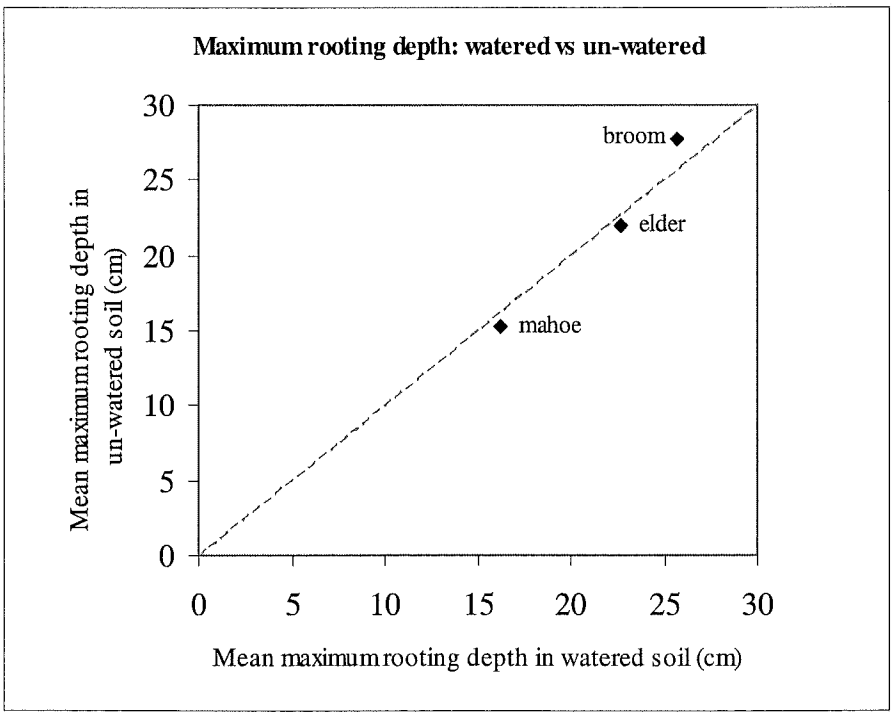


Figure 6.6. Maximum rooting depth of broom, elder and mahoe under well-watered and un-watered treatments. (The dotted line shows no difference in treatments (1:1)).

The percentage of root biomass distribution at different depths is shown in Figure 6.7. Most of the root dry weight was distributed in top levels of the soil down to 20 cm. Elder and mahoe roots were not found deeper than 30cm. Broom roots penetrated to deeper levels than elder and mahoe, although the percentage of root biomass was very low at the deepest level; 4.2% in the watered treatment and 6.8% in the un-watered treatment. In upper levels of the soil (up to 20 cm) the percentage of broom root biomass was greater in the watered treatment than the un-watered treatment. The opposite was true at the lower levels (20-30 cm and 30-40 cm). Both elder and mahoe root biomass was quite similar up to 20 cms. Root biomass for mahoe and elder was greater in the watered treatment than the un-watered in soil depth 20-30 cm.

Biomass partitioning between root and shoot components followed a similar pattern to the water stress experiment, increasing root /shoot ratios in un-watered treatments for broom and mahoe while elder showed slight decrease in the un-watered treatment (Figure 6.8). However, root/shoot ration was not significantly different between treatments.

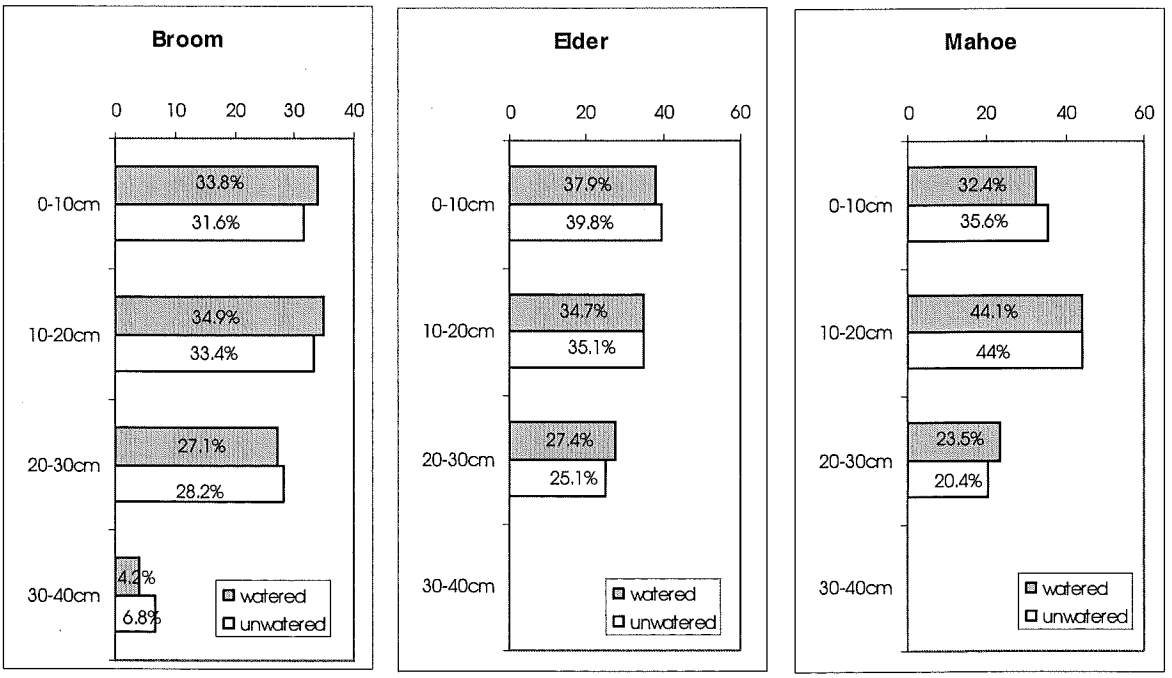


Figure 6.7. Distribution of root biomass of broom, elder and mahoe under watered and un-watered treatments.

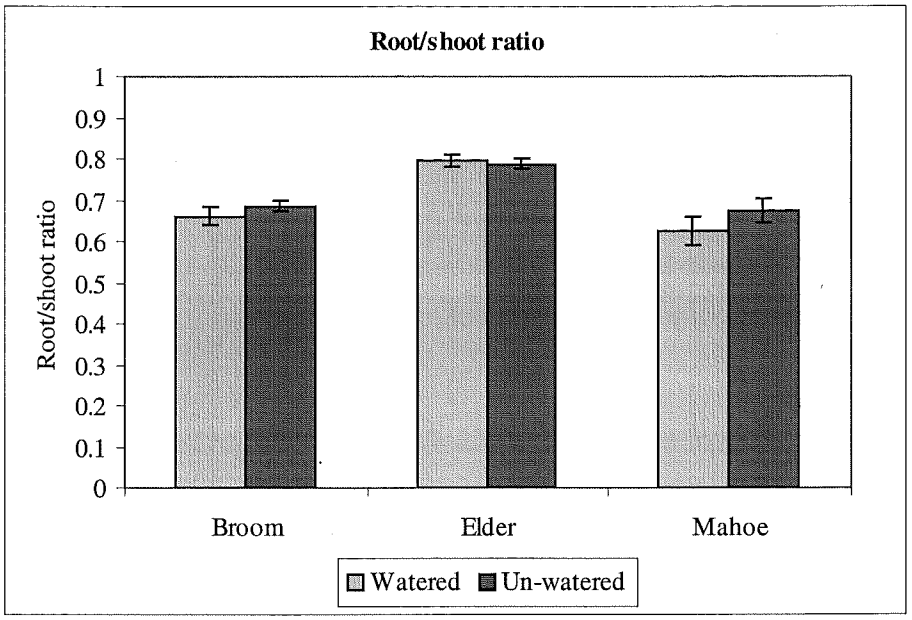


Figure 6.8. Biomass partitioning between root and shoot components of broom, elder and mahoe under watered and un-watered treatment.

6.6.4. Discussion

Experiment 3 was undertaken to test root growth under water stress. The results obtained from the trial revealed clear differences in rooting habits between broom and the other two species in response to water limitations. Root plasticity significantly increased the distribution of root dry weight in deeper soil levels of broom, enhancing the ability to search for water. In both elder and mahoe, maximum root penetration under the un-watered treatment was less than in the watered treatment. In mahoe the reduction in maximum root penetration was significantly different between watered and un-watered treatments (Table 6.11, Figure 6.6).

During seedling establishment, survival is very much dependent upon access to moisture. The ability to obtain water in comparatively deeper soil is important and evidence suggests the physiological plasticity of roots enhances water absorption. Results from this experiment agree with other studies of root plasticity and root/shoot

ratios. Molyneux and Davies (1983) found an increase in rooting depth in pasture grasses growing in drying soil. Sharp and Davies's (1985) study on maize plants also showed an increase in root depth with increased soil moisture stress. Reader *et al.* (1993) reported a positive relationship of plasticity in root penetration and the ability to sustain growth in drying soil in a comparison of 42 vascular plants.

Of the three species studied, broom appeared to have an advantage over elder and mahoe in reaching water at deeper levels. Bannister (1986) reported broom did not wilt at the sites where other species were stressed. Broom can recover from wilting without damage by developing a low water potential (Bannister 1986). Having a deeply penetrating root system and an increased plasticity under conditions of water stress suggests an added feature for drought tolerance of broom and would be suitable for the conditions of exposed sites.

6.7. Experiment 4: Seed germination under different soil water stress

6.7.1. Introduction

The natural regeneration of plant species depends upon the production and germination of seeds and successful establishment of seedlings. Water stress is one of several abiotic factors (e.g. temperature, light) that has a significant effect on seed germination (Rao and Singh 1985; Rao 1988). Water is directly involved in the timing and rate of seed germination in field conditions. Emerging-seedling survival is more likely if seed germination can take place when the soil water is sufficient to ensure an adequate supply of water to satisfy the demand of young seedlings (Etherington 1993).

Determination of the effect of water stress on seed germination was expected to provide an insight into the relative capacity of broom, elder and mahoe to germinate under different soil water levels. An understanding of this physiological capacity

could then be related to their successional positions. Experiment 4 complements the germination experiments reported in Chapter 4. The method described here was adopted from Etherington (1993).

6.7.2. Materials and methods

Soil was passed through a 2 mm sieve then thoroughly mixed and watered to saturation. Thirty six small polyurethene foam trays were filled with the moistened soil. The tray dimensions were 20 cm length, 8 cm width and 2cm depth. The trays were divided into four groups for four treatments each containing nine trays. The nine trays of each treatment were divided into three groups, with three replicates for each species.

The seeds used in this experiment had been stored at room temperature in sealed polythene bags for 6-9 months. Seeds were gently scarified using fine sand paper and fifty fully formed seeds from each species were selected and slightly buried (approximately 0.5 cm) on each tray in 5 rows (10 seeds per row). Broom and mahoe trays were placed in one growth cabinet at 20^0C/12hr light/ 60% relative humidity (r.h.) and 18^0C /12hr dark/ 65% r.h. Elder trays were placed in another growth cabinet at 20^0C for 8 weeks and under 4^0C thereafter under 12hr light at 60% r.h/12 hour dark at 65% r.h, because elder requires temperature stratification for germination. Trays were covered to reduce evaporation.

6.7.2.1. Treatments

Four soil water treatments were used:

1) T1: 200 ml of water was sprayed onto each tray daily;

2) T2: 100 ml of water was sprayed onto each tray daily;

3) T3: 50 ml of water was sprayed onto each tray daily;

4) T4: 25 ml of water was sprayed onto each tray daily;

The amount and frequency of water added to the treatments was decided following several preliminary trials. The selected levels and frequencies yielded a considerably different soil water content yet seed germination could still occur. The soil water content of each treatment was monitored using eight soil trays filled and treated exactly as for the treatments. Four of these trays were kept in each of the two growth cabinets used for the experiment. Soil samples from these trays were taken weekly to determine soil water content. Samples were taken prior to watering. Average water contents in the treatments during the experiment were; 34.2% (T1), 29.3% (T2), 24.4% (T3) and 18.9% (T4).

Water was sprayed close to the soil surface in order to reduce loss of water into the air but care was taken to avoid altering the positioning of the seeds. Towards the end of the experiment the soil water content of some treatments was observed to decrease. This appeared to be due to prolonged germination times, especially of elder. Therefore the amount of water added was slightly adjusted after 6 weeks.

6.7.2.2. Measurements

Trays were examined daily when watering. The time taken to the onset of germination was recorded and the number of germinated seeds counted. After counting, germinated seeds were removed from the experiment and at experiment termination, un-germinated seeds were tested with TTC (triphenyltetrazolym chloride) for viability. The experiment was terminated approximately two weeks after showing no further germination, depended on the species. For example, broom and mahoe stopped further germination approximately 60 days into the experiment while for elder, the experiment terminated after 22 weeks.

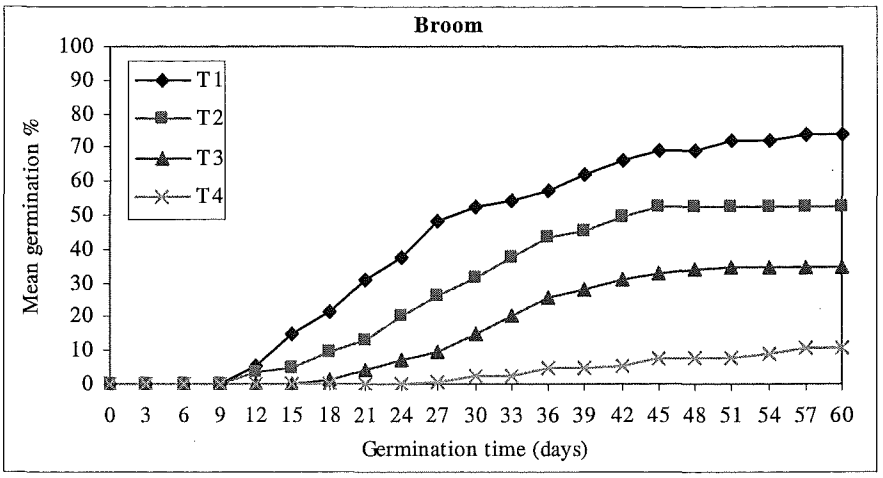
6.7.3. Results

SAS GLM procedures showed that seed germination was significantly influenced by species ($F(2,33)=5.2$, $P\leq0.05$) and treatments ($F(3,33)= 35.5$, $P\leq0.001$). Further analysis revealed germination of broom significantly different between treatments

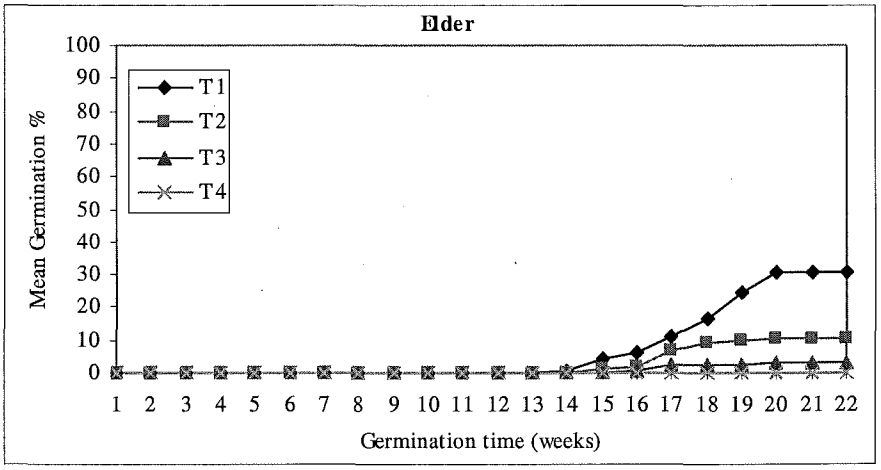
($F(3,8)=90.3$, $P\leq0.001$). The maximum germination showed in broom was 74% in T1. Seed germination was decreased to 53% (T2), 35% (T3), and 10.6% (T4) with decreasing soil water content (Figure 6.9a, Table 6.12).. Only broom was capable of germination in T4 with 10.6% where mean soil water content was dropped down to 18.9% (Figure 6.9). Elder germinated poorly even in T1, achieving a maximum of 30.6% (Figure 6.9b) and germination dropped to 10.6% and 3.3% in T2 and T3, and 0% in T4. The decrease in germination percentage between treatments were significant ($F(3,8)=188.8$, $P\leq0.001$). Mahoe seed germination dropped significantly ($F(3,8)=382.6$, $P\leq0.001$) with decreasing soil water. The maximum germination recorded for mahoe was 76% in T1 and germination was reduced to 25% (T2), 6% (T3) and 0% (T4) (Figure 6.9c). Tukey's test results showed that germination of broom, elder and mahoe were significantly different in all treatments (Table 6.12).

The time taken to the onset of germination significantly increased with decreasing soil water content. Tukey's test revealed that the increase in time required to start germination was not significantly different between T1 and T2 in all species while in other treatments the time to onset of germination was significantly increased (Table 6.12).

a)



b)



c)

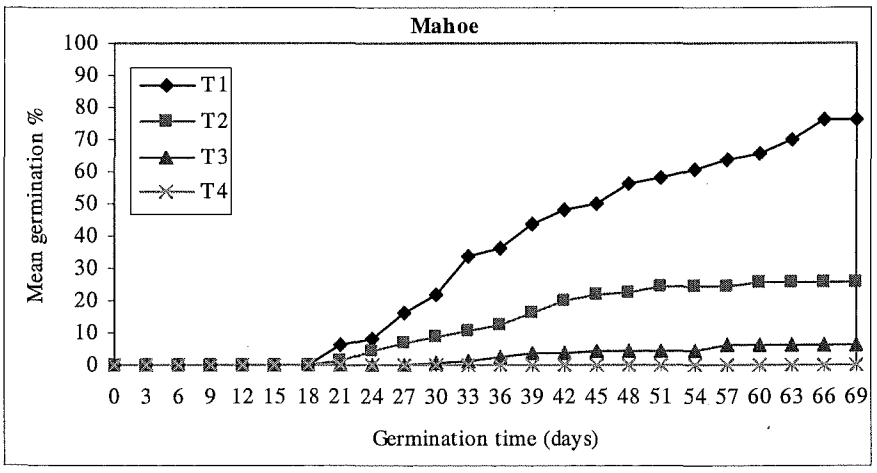


Figure 6.9. Seed germination of a) broom b) elder and c) mahoe under different soil water levels. (note: different X axis labels)

Table 6.12. Seed germination of broom, elder and mahoe at different soil water treatments Tukey's test comparisons. (Same letters in comparisons indicate that the means between comparisons are not significantly different at P≤0.05; n.g =no germination).

Treatment	Mean number germinated	%	Rate (50 seeds $seed^{-1}$ day^{-1})	Mean time to onset of germination (days)
Broom				
T1	37±2.08 a	74 a	0.789 a	12 a
T2	26±0.88 b	52.6 b	0.598 ab	13 a
T3	17.3±0.88 c	34.6 c	0.400 b	20 b
T4	5.3±1.45 d	10.6 d	0.099 c	29 c
Treatment	Mean number germinated	%	Rate (50 seeds $seed^{-1}$ $week^{-1}$)	Mean time to onset of germination (weeks)
Elder				
T1	15.3±0.88 a	30.6 a	0.7798 a	14.6 b
T2	5.3±0.33 b	10.6 b	0.285 b	15.3 ab
T3	1.6±0.33 c	3.3 c	0.093 c	16.6 a
T4	n.g	n.g	n.g	n.g
Treatment	Mean number germinated	%	Rate (50 seeds $seed^{-1}$ day^{-1})	Mean time to onset of germination (days)
Mahoe				
T1	38±1.15 a	76 a	0.584 a	21 a
T2	13±1.2 b	25.3 b	0.262 b	22 a
T3	3±0.5 c	6 c	0.059 c	33 b
T4	n.g	n.g	n.g	n.g

6.7.4. Discussion

Experiment 4 was intended to simulate conditions that a seed might face in the environment after shedding from the parent plant. Broom showed pronounced differences in the ability to germinate under the tested soil water conditions than did elder and mahoe. Broom was capable of germination (10.6%) in the lowest soil water content treatment (18.9%). This feature may help broom to germinate in open and exposed sites where soil water content is low in the top regions of the soil.

The ability to germinate and emerge successfully is an important adaptation for sites with fluctuating water levels such as upper regions, open sites (Crawford 1989). The water application pattern in this experiment provided seeds with periods of wet and dry soils during a day (especially T4). The germination performance of broom in T4 suggests that broom seeds are better able to withstand fluctuations of desiccation and hydration that may prevail in exposed sites. Cycles of favourable and unfavourable conditions of hydration experienced in exposed sites, might serve as germination cues for gap detection (Fenner 1985).

The ability to germinate in water limiting conditions, however, does not guarantee successful establishment. Successful establishment depends on a seedling's ability to tolerate different water stress levels. As discussed in Section 6.4.4, broom seedlings are more tolerant of water stress than elder and mahoe. Therefore, broom could successfully germinate and establish under water limiting conditions more readily than the other two species in the sequence. These features can be considered useful in establishment at exposed sites.

Alternatively, elder and mahoe proved their inability to germinate satisfactorily under water limiting conditions, suggesting poor suitability at drier sites. Both elder and mahoe showed very low germination (3.3% and 6% respectively) in T3 where soil water content was 24.4%.

In general, all species showed comparatively lower final germination even in the highest soil water content treatment (T1) of this trial than in the seed germination trials reported in chapter 4 of this thesis. This reduction in germination may be due to the use of un-hydrated air-dried seeds in the experiment. Because of this, the seeds had to overcome resistance to water movement through the unsaturated seed soil surface rather than gradient of soil water content. However, Etherington (1993) reported soil as the medium was more ecologically realistic. The exact orientation of the seed on the soil may also affect the germination (Sheldon 1974).

6.8. Experiment 5: Determination of water use efficiency

6.8.1. Introduction

Most plants suffer under some degree of water stress from time to time and as a result reduce the rate of CO_2 fixation by stomatal closure or changes in cell metabolism. However, stomatal closure results in a reduction in transpiration necessary to maintain leaf temperature and nutrient uptake. The relationship between water loss through transpiration and biomass production is a measure of the adaptation of a plant to its environment and can be measured by water use efficiency. Plants with high water use efficiencies have a better chance of survival and establishment in dry conditions than plants with low efficiencies although there is no direct link between water use efficiency and water stress tolerance (Kramer 1983). A comparison of water use efficiency in this experiment was expected to identify the relative water economy of these species.

Water use efficiency is defined in number of ways. Kramer and Boyer (1995) defined water use efficiency as the total dry matter produced by plants per unit of water used and can be illustrated as:

$$WUE=D/W \quad \text{.....Equation(6.3)}$$

where WUE is water use efficiency, D is the mass of dry matter produced and W is the mass of water used. According to Equation 6.3, the higher dry matter production per unit of water use, the higher the efficiency. Teare *et al.* (1973) termed water use

efficiency as the amount of water used (both by evaporation and transpiration) per unit of biomass and can be expressed as;

$$WUE = \frac{\text{Accumulative evapotranspiration}}{\text{Biomass produced}} \quad \text{.....Equation (6.4)}$$

According to the above equation, a high water use efficiency value actually describes a low water use efficiency because evaporation, which largely depends upon environment, is also counted. An estimation of WUE can also be given as a Water use index (WUI) (Sun 1993; Roberts and Schnipke 1994). Roberts and Schnipke (1994) used changes in plant size index (SI) per total average irrigation demand (AID) to determine WUI. Sun (1993) also used water use index (WUI) in expressing plants water use efficiency; accumulative transpiration per unit biomass produced and expressed as,

$$WUI = \frac{\text{Accumulative transpiration}}{\text{Biomass produced}} \quad \text{.....Equation (6.5)}$$

Accumulative transpiration was calculated by subtracting total water loss from evaporation and therefore WUI was expressed as:

$$WUI = \frac{\text{Total water lost-evaporation}}{Wt - Wo} \quad \text{.....Equation (6.6)}$$

Where,

Wt-final dry matter weight
W0- initial dry weight

This study used equation 6.6 to calculate the water use index.

According to this equation the higher the transpiration per unit biomass, WUI tends to increase. Therefore plants with high WUI use water less efficiently than those with low WUI.

6.8.2. Materials and methods

6.8.2.1. Seedling Preparation

Seeds of each species were grown under glasshouse conditions. Twenty seedlings from each species were chosen as described in section 5.4.3.1 and fifteen seedlings of each species were used for the experiment and the rest was used to obtain initial dry weights.

6.8.2.2. Method

The seedlings were transplanted into plastic pots (10.5 cm internal diameter x 13 cm high) with drainage holes in the bottom. They were filled with potting mix packed to a bulk density of approximately 1.1 g cm $^{-3}$. Pots were watered to field capacity and randomly arranged on a glasshouse bench. The surface of each pot was covered with a black polythene disc to minimize evaporation. All pots were weighed at the beginning of the experiment and weekly thereafter. Water loss due to evapo-transpiration was calculated and replaced (after weighing the pots) by watering back to field capacity. Two hours after watering the pots were re-weighed and any water collected in the saucers placed under pots was deducted from the amount of water added. Pots were re-arranged weekly after watering. The experimental time was 12 weeks. Five additional pots filled with same amount of potting mix, treated identically (weighed and watered weekly to the field capacity) as the pots in the actual experiment were used to determined the evaporation from the soil surface during the experimental period (12 weeks).

At the end of the experiment, plants were harvested and total biomass (shoot and root) was measured after drying at 80^{0}C for 48 hours. Total water loss by transpiration was calculated using the total water added and evaporation in each pot over the experimental period. Water use index was calculated according to equation 6.6.

6.8.3. Results

The results show an increase in the water use index from broom through elder to mahoe. Mean water-use index for broom during the experimental period (12 weeks) was 260.9 (±6.9) while for elder and mahoe the mean values were 296.3 (±8.4) and 330.3 (±13.0) respectively. Elder's WUI was 13.6 % higher than that of broom while mahoe's WUI was 26.6 % higher than broom.

Single factor analysis of variance procedure revealed that WUI was highly significantly different between species ($F(2,42)=12.45$, $P\leq 0.001$). Tukey's test to compare species means showed significant differences in WUI of all species. The results of this experiment are summarized in Table 6.13.

Table 6.13. Water use index of broom, elder and mahoe. (Means designated by the same letter are not significantly different based on Tukey's test ($P\leq 0.05$)).

Species	Mean WUI ($g\ g^{-1}$)	Minimum	Maximum	Significance
Broom	260.9 (±6.9)	220.8	302.5	a
Elder	296.3 (±8.4)	214.7	331.8	b
Mahoe	330.3 (±13.0)	277.8	454.9	c

6.8.4. Discussion

Low WUI value in broom means a relatively small amount of water was transpired per gram of dry matter produced; comparatively higher values in elder and mahoe mean that they use more water per biomass produced. This shows that water-use efficiency decreased from broom >elder>mahoe.

Species morphology, water stress tolerance and root systems may explain differences in WUI. Smaller leaves at the seedling stage and the elimination and reduction of leaves at later stages may reduce water loss through transpiration from broom and as a result lower the value of WUI. Alternatively the narrow and shallow root system of mahoe (as mentioned in Section 6.6.3) and relatively broader leaves may enable more transpiration and less absorption under water stressed conditions compared to broom and, thus result in low efficiency.

Although results from this experiment show clear differences of water use between species, there are concerns about the importance of water use efficiency in determining plant performances beyond an agronomic context such as in the natural environment. For example, Jones (1993) mentioned that having a high water use efficiency (and therefore conservation of water by some plants in a natural environment) would have no advantage for a plant as competitors could then use the available water. However, once water has been captured, having a high efficiency of water use could still be an advantage in natural environments.

6.9. Conclusions

The relative water requirement of broom, elder and mahoe was assessed through five laboratory/ glass-house based experiments in order to relate their position in the successional pathway of broom through elder to mahoe. Water stress tolerance at the seedling stage, plant relative water contents, seed germination under different soil water contents, maximum root penetration and water use efficiency of broom, elder and mahoe were tested. Differences between broom, elder and mahoe in water relations were identified. The following conclusions can be drawn from these experiments.

1). Broom seeds were more readily able to germinate under water stress conditions than elder and mahoe. The inability of mahoe and elder to germinate when soil water content fell below 19% (and the very small percent germination at 26% water content) prevents germination of these species at low soil moisture levels. Therefore,

it is suggested that mahoe and elder seeds are more likely to germinate in moist conditions (e.g. under shade) than open areas where soil moisture is reduced by evaporation.

2). The maximum rooting depth that the root systems of each species reached increased in the order of mahoe<elder<broom. The shallow and narrow root system of mahoe restricts accessibility to water at deeper levels and as a consequent, makes mahoe intolerant of water limitations. Root penetration was negatively affected by increasing water stress both in elder and mahoe. Broom root penetration significantly increased with water stress.

3). Broom is able to withstand lower levels of leaf water content than elder and mahoe before showing signs of wilting. Mahoe reached permanent wilting point more quickly than either elder or broom.

4). Broom used water resources more efficiently than elder and mahoe, giving broom an increased opportunity to function normally under water stress conditions. This ability is advantageous to species that establish in open sites. Elder and mahoe require more water in order to function normally, which makes it difficult for them to establish in dry conditions.

Early stages of secondary successional sites often face water stress conditions, at least in the upper layers of the soil due to direct exposure or pasture coverage. From the results of this chapter, it can be suggested that broom is better able to establish and function more normally than both elder and mahoe, in open pasture sites with lower soil moisture levels. Therefore broom can be regarded as a favoured species for early successional sites in the Hoon Hay Valley region where summer droughts are also common. Furthermore, the comparatively poor performance of elder and mahoe suggests that these species are better suited to less exposed sites, possibly as sub-canopy species.

Chapter 7

General discussion

7.1. Introduction

This study investigated in detail one successional pathway which has been proposed following field observations (Williams 1983). Major factors and aspects generally considered important in the successful arrival, establishment and survival of a plant in a particular habitat include seed characteristics, light, nutrient, and water requirements. The study was built upon three hypotheses and several experiments have been presented to test aspects of these sets of hypotheses. Chapter 7 integrates and discusses the research findings presented in this thesis.

7.2 Hypotheses

7.2.1. Seed characteristics

Hypothesis 1:

The order of species in the broom→elder→mahoe succession is dependent on seed characteristics.

— Seed size should increase from broom<elder<mahoe.

— Seed food reserve should increase from broom<elder<mahoe.

— Seed longevity should decrease from broom>elder>mahoe.

— Light requirements for germination should increase from broom>elder>mahoe.

— Dormancy breaking requirements are related to the successional positions of broom, elder and mahoe.

— Seedling's ability to emerge from deeper soil levels should decrease from broom>elder>mahoe.

A seed is the start of a new plant and successful germination depends on a seed being in the 'right place' at the 'right time'. The production of an excess of seeds in combination with appropriate dispersal mechanisms ensures seeds are not only widely dispersed, but also increases the chances of seeds landing in the 'right place'. In general, early successional species dispersed by wind tend to have lighter seeds (Fenner 1987). According to the postulated successional sequence (Williams 1983), if broom is an early successional species, it would be expected to have lighter seeds than those species arrive later. The prediction that the seed size should increase from broom<elder<mahoe was not substantiated by the research as broom had the highest seed weight of the three species tested. The main dispersal mechanism for broom is pod dehiscence (60%-80% pods) although several secondary dispersal pathways (e.g. ants) are known for broom (Smith and Harlen 1991).

The germination requirements for broom suggest a capability of germination irrespective of light (although at a slower rate in the dark) and higher overall germination rate than elder and mahoe. Light sensitive seeds are generally associated with early successional species and this mechanism prevents seeds germinating under canopies where photosynthetic processes are restricted. The lack of a light requirement for germination may suggest the successional position of broom may be further along the successional pathway than initially postulated or that light is not a determining factor in broom's success as a colonizer. Furthermore, the disadvantage of germination under a light restricting canopy may be compensated by larger food reserves in heavier broom seeds.

Alternatively, it can be suggested that early successional species need not necessarily be light-weight and wind-dispersed, especially in a secondary succession. For instance, where a gap is created in existing vegetation, there is no dependence on seeds arriving from elsewhere, because there is a seed bank present in the soil awaiting favourable germination conditions. In fact this situation may be more appropriate in the Hoon Hay Valley because successional processes underway are due to disturbances such as fire and farming on previous vegetation. In addition, the present study found 94% broom seeds remain viable after two years of storage, reflecting an active soil seed bank even though in the field the viability might be decreased due to fungal decay. Field studies also shows a persistent buried soil seed bank for broom (Partridge 1989) that have over 50% viability after 4 years (Smith and Harlen 1991) and even a few seeds remained viable after 81 years (Turner 1934). Moreover, the present study also found that a higher percentage of broom seeds were able to emerge from comparatively deeper levels of soil than the other two species, thereby indicating the relative efficiency of the soil seed bank.

The position of broom in the successional pathway is not clear, making a confirmation of the position suggested by Williams (1983) difficult. As far as the seed characteristics of broom are concern, the possibilities are:

a) Broom is an early successional species although it had some characteristics found in mid to late sucessional species.

b) Broom has versatile seed characteristics and therefore it may be suited to both early and later succession. The actual successional position of broom may be determined by some other factor.

Williams (1983) positioned elder in between broom and mahoe in the successional sequence. Elder seed size is intermediate between broom and mahoe, which is contrary to the generalization of seed size increase with successional advance. Overall the seed germination of elder was poor, requiring temperature stratification in order to break dormancy and then only achieving a maximum of 60% germination. These results suggest, under field conditions the requirement by elder for stratified temperature bring about an annual seasonal cycle for germination. Seed characteristics alone cannot explain the successional position of elder. The ability of seeds to remain viable (in relatively higher percentages) would be an advantage; after an annual seasonal cycle, viable seeds in the soil seed bank are then ready to germinate and establish. Observations on the dispersal modes explain the successional position of elder more readily than the requirements for germination. For instance, a vast amount of fruit is produced giving an ample supply of seeds and the edible fruits attract birds and other dispersal agents. Birds facilitate the arrival of other adventive species at a site through their droppings (Voyce 1998). The possession of edible fruits in conjunction with animal-aided dispersal is a characteristic feature of seeds of mid to later successional species. Although elder is slow in the initiation of germination, the poor overall germination rates do not appear to be a problem, considering the relative abundance of elder in the Hoon Hay Valley (e.g. Dungan 1997; O'Cain 1997; Voyce 1998).

According to the proposed successional pathway, mahoe arrives last and could be expected to have different seed characteristics than broom and elder. As mahoe has the smallest seeds of the species tested, the food reserve in the seed can only provide limited support for seedlings emerging in the new environment. In the later stages of succession, light at ground level is limited due to canopy closure and therefore seedlings face stressed conditions unless they are shade tolerant. The ability of mahoe to germinate in the dark appears to be linked to bird dispersal. Other germination studies suggest that many bird-dispersed native species are able to germinate in the dark (Burrows 1995 a, b, c; Burrows 1996 b, c). Frugivorous birds deposit droppings under the trees they are feeding or perching on. The micro-environment under trees is often dark, suggesting many bird-dispersed seeds are adapted to survive in the shade for several years (Smith 1975). However, success depends also on a seedling's ability to survive in the limited light as there are great variations in the shade tolerance of seedlings of bird-dispersed seeds (Williams and Buxton 1989).

The viability of late successional species decreases soon after dispersal, largely due to their vulnerability to predation and they do not form a soil seed bank with dormant seeds (Fenner 1987). This is also an adaptation to prevent seeds from germinating in poorly-lit sites. An alternative strategy of late successional species is to maintain populations of saplings with their growth suspended to compete in quickly closing canopy gaps (Fenner 1987). Dungan (1997) reported a large number of mahoe saplings under canopies in the Hoon Hay Valley.

Mahoe seeds remained viable in considerable numbers and they are prominent in soil seed banks (Partridge 1992). Mahoe may be more suited to mid successional stages where soil nutrients and light are not so limited. The disadvantage of having smaller seeds could be counterbalanced by a reduced competition for light and nutrients.

All plant species discussed in this study have versatile seed characteristics and are able to germinate in open or shaded sites. No justification was found to explain why mahoe seeds would not be able to germinate in an open site or broom in a later successional site if seeds are already present at the site. However, arrival to a site is also crucial and the type of fruit that these plants produce has a greater role here. The edible berries of both elder and mahoe made them attractive for birds. Williams (1983) described how broom facilitates the arrival of elder by providing preferred perching locations on their open twiggy crowns for birds. Elder then acts similarly to facilitate the entry of mahoe (Williams 1983). The sequential positions of species in the successional pathway suggest mode of arrival and versatility in germination are key factors to be considered.

The hypothesis that the species sequence in the successional pathway is dependent on differences in seed characteristics the species cannot be rejected; there is some evidence to suggest that broom is early successional while other two species appear later in the sequence.

7.2.2. Light and nutrient requirement

Hypothesis 2:

That the order of species in the broom→elder→mahoe succession is dependent on the differences in light and nutrient requirements of each species.

— Seedling tolerance of shade should increase from broom<elder <mahoe.

— Seedling nutrient requirement should decrease from broom>elder>mahoe.

— Allocation to shoots in the shade should decrease from broom>elder>mahoe.

The competition for resources is a very important underlying rule of succession. Plants require light, mineral nutrients, water and carbon dioxide for their functioning and plants provide resources for herbivores, parasites, pathogens and predators

leading to plant loss and mortality. In addition, there are disturbances to habitats. Within a given habitat, plants are restricted by resource availability and loss or mortality caused by disturbance and predation. The success of a plant depends on how well limited resources are utilized and the trade off of maintaining a competitive growth rate. This trade off is a dominant cause of vegetation patterns in natural communities (Tilman 1988). The resource isocline theory for vegetation succession assumes that when resources are limited, competition occurs with the outcome dependent upon the relative resource requirements of individuals. When several species are limited by a single resource, the species with the lowest resource requirement at which the net rate of population change is zero, competitively displaces other species (Tilman 1988).

The open sites at the Hoon Hay Valley have a higher availability of light. Broom with light sensitive seedlings, could establish and grow successfully. Light would become limiting as broom grows higher and at this point, further growth would be suppressed by other species, such as elder. As succession advances the light resource becomes more limiting and shade-tolerant species such as mahoe would have an advantage over other species, displacing them from the habitat.

The dynamics of the light-dependent growth of species in a successional pathway can also be explained by Connell and Slatyer's (1977) facilitation model where early successional species modify the physical environment to a point where it is no longer suitable for the species, but becomes more suitable for later species. The physical environment is modified from the open stage (with more light) to a shaded place (with less light) resulting in selection for the species which have characteristics favourable to a shaded place.

Significant differences were identified in the light requirements for successful growth of broom, elder and mahoe. Broom grows rapidly under full-light conditions and growth is significantly affected when light levels decreased. The experiments suggest an order of decreasing demand for light from broom> elder> mahoe. These

results are in accordance with other findings on the light requirements of these three species (e.g. Tansley 1939; Williams 1981; Williams and Buxton 1989; Roxburgh 1992).

Under natural conditions, more than one resource can be limiting at any one time. For example, experiment 2 (Chapter 5) examined the effect of both light and nutrients (nitrogen and phosphorus). Broom was found to have not only a sensitivity for low light but also for low nutrients; it should therefore be more competitive where light and soil nutrients are rich (such as open sites on rich soil). Broom also has the capability of fixing atmospheric nitrogen. Soils in the Hoon Hay Valley are classified generally as moderately acid, low in available phosphorus, moderate in exchangeable cations and of medium to good fertility (Fitzgerald 1966; Hewitt 1993). If a site with such fertility becomes open after a disturbance, broom could gain the advantage and establish well. The loss of broom from the vegetation could be a result of the effect of decreasing light as well as nutrients, as with the advancing succession, availability of these resources tend to decrease with a parallel increase in demand. Phosphorus significantly influenced the growth of broom and is known to be low in Hoon Hay Valley soils. It is important to note that the growth rate of both elder and mahoe was not significantly affected by different phosphorus levels indicating these species are able to tolerate P fluctuations with less affect on growth. However, both these species showed a sensitivity to nitrogen. If mahoe is a later successional species (considering its shade tolerance and less demand for P) it would face a problem of nitrogen shortage as nutrient availability decreases in the later stages of succession due to increased demand, or a reduction in the rate of decomposition, due to changes in microclimate. Therefore it is possibile that mahoe might not represent a late succesional stage and instead perhaps be associated with mid successional stages (where nutrients are less restrictive). Resource availability in the mid successional stages may even increase (for a number of years) due to the rapid growth and high nutrient contents of early successional species which feed-back into the system favourably through rapidly decomposing litter material (Vitousek and Walker 1987). An early successional species with an ability fix

atmospheric nitrogen, broom could contribute to an increase in nitrogen levels in mid successional stages as explained by Vitousek and Walker (1987) thereby providing better environmental conditions for mahoe.

The hypothesis that the species sequence in the successional pathway is dependent on differences in light and nutrient requirements of the species cannot be rejected although the actual successional stages they are supposed to be representative of may be slightly different.

7.2.3. Water requirements

Hypothesis 3:

That the order of species in the broom→elder→mahoe succession is dependent on the differences in water relations of each species.

— Seedling water stress tolerance should decrease from broom>elder>mahoe.

— Seedling relative water content under water stress conditions should increase from broom<elder<mahoe.

— Seedling root penetration under water stress conditions should decrease from broom>elder>mahoe.

— Seed germination under water stress conditions should decrease from broom>elder>mahoe.

— Seedling water use efficiency should decrease from broom>elder>mahoe.

Plants in early successional habitats are fast-growing, short-lived, have a high reproductive output (Bazzaz 1987) and broader responses to resource gradients than mid and later successional species due to large fluctuations in local resource availability (Odum 1969). Bazzaz (1987) compared the responses of plant species from different successional communities to soil moisture gradients and responses

were measured in terms of germination, survivorship and growth of vegetative and reproductive biomass. It was found that the responses to soil moisture gradients of early successional species are broader and overlap more than later successional species.

In a disturbed site, transpiration is reduced. Evaporation from the soil surface increases after a disturbance due to an increase in light intensity, soil surface temperature and wind; the soil surface become drier and the water table is raised compared to undisturbed sites (Bormann and Likens 1979). The water-holding capacity of the soil is known to vary less in secondary succession than in primary succession (Vitousek and Walker 1987).

In this study the water requirements of the three species were found to be markedly different, affecting their ability to perform under water limiting conditions. Following a disturbance, water availability in an open site could be expected to decrease. The germination and establishment of species at such sites is difficult and plants need suitable adaptations for such conditions. When resources are limited, the species with a minimal resource requirement would be better able to withstand the conditions and displace others (Tilman 1988). The study found the minimum water requirement for germination was lower for broom than elder and mahoe, suggesting broom seeds in an open site are more favoured to survive. The effect of water stress on seedling growth decreased in the order of elder>mahoe>broom. Broom seedlings were able to allocate more biomass to their roots under stressed conditions and the depth of root distribution was highest in broom. Even though elder had a fairly large root system it was shallowly distributed. The root system of mahoe seedlings was deeper than elder although not widely spread. A deep root system is an advantage when establishing in open sites, as open sites tends to dry out quickly due evaporation from the surface and deep roots would be able to acquire water from deeper levels. Open sites are at risk from wind damage, so deep roots may help a plant to withstand damage. The inability of elder seedlings to tolerate water stress might be due to their shallow (although widespread) root system. Water stress

tolerance of broom seedlings were also due to their ability to maintain comparatively lower relative water contents under water limiting conditions. In addition, broom had the highest efficiency of water use. Because of these characteristics, broom has a higher chance of survival under the harsh conditions of open sites. The high water requirement of both elder and mahoe restrict them to locations where the water level undergoes relatively less fluctuation.

Droughts are common in the Hoon Hay Valley, especially in late summer months and the well-drained soils become dry particularly on the north facing slopes (Williams 1983). Therefore on the open sites, where early secondary successional species become established, it is possible to expect severe moisture deficit conditions from time to time and this study suggests that broom is well-equipped to handle such situations. Similarly, the water requirements of elder and mahoe are better suited to sites with minimal water fluctuations.

The hypothesis that the order of species in the broom→elder→mahoe succession is dependent on the differences in water relations of each species cannot be rejected; instead the study revealed marked differences in water requirement of the three species that are suitable to conditions in different successional stages.

7.3. Summary diagrams

The results are summarized in diagram form in Figures 7.1, 7.2 and 7.3, which assess the suitability of each species for different stages of succession. Broom has more favourable characteristics for conditions in the early stages of a secondary succession (Figure 7.1) whereas both elder (Figure 7.2) and mahoe (Figure 7.3) characteristics are more favourable for conditions in mid or/and later succesional stages.

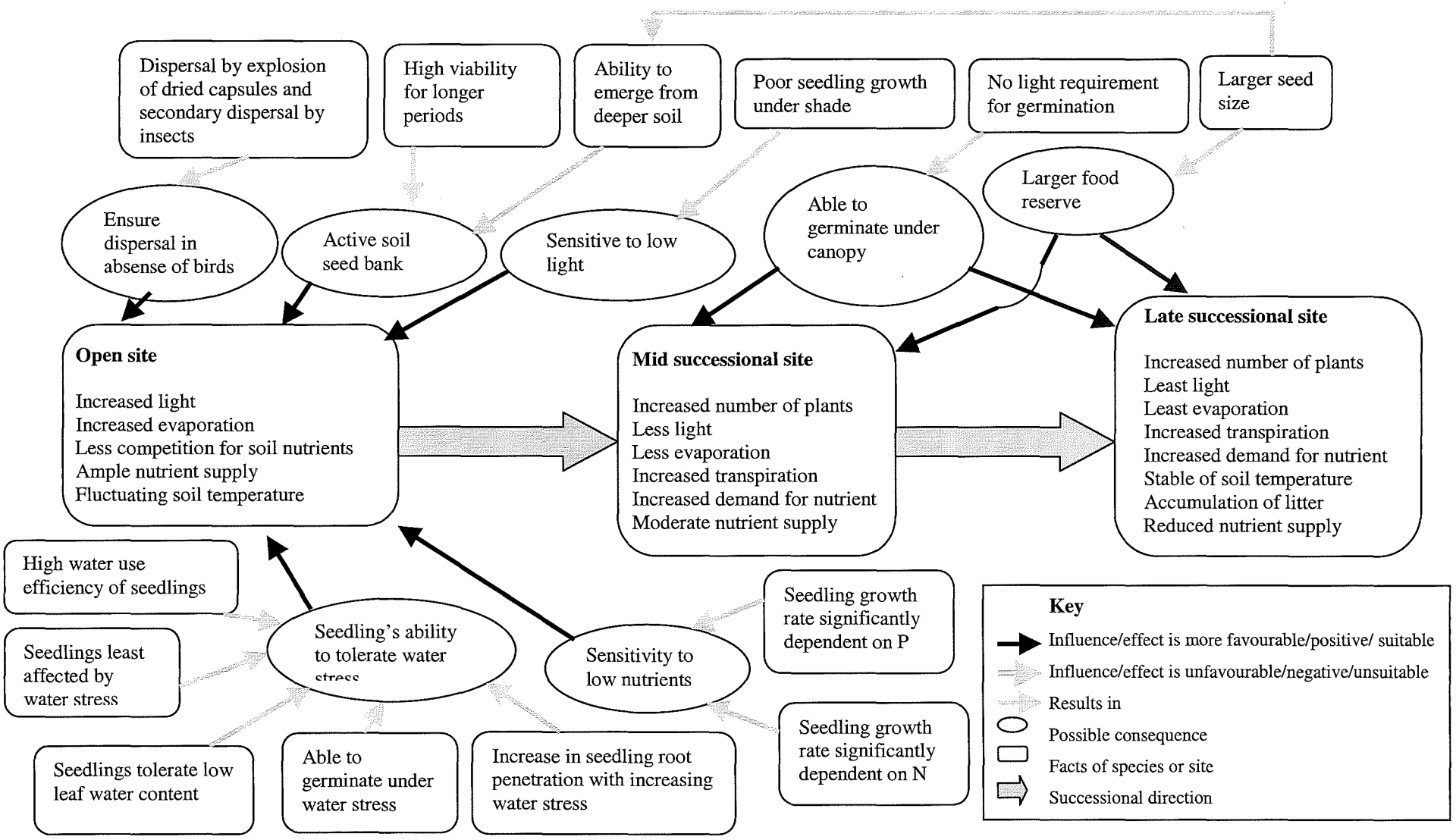


Figure 7.1. Assessing suitability of broom seeds and seedlings to different successional stages

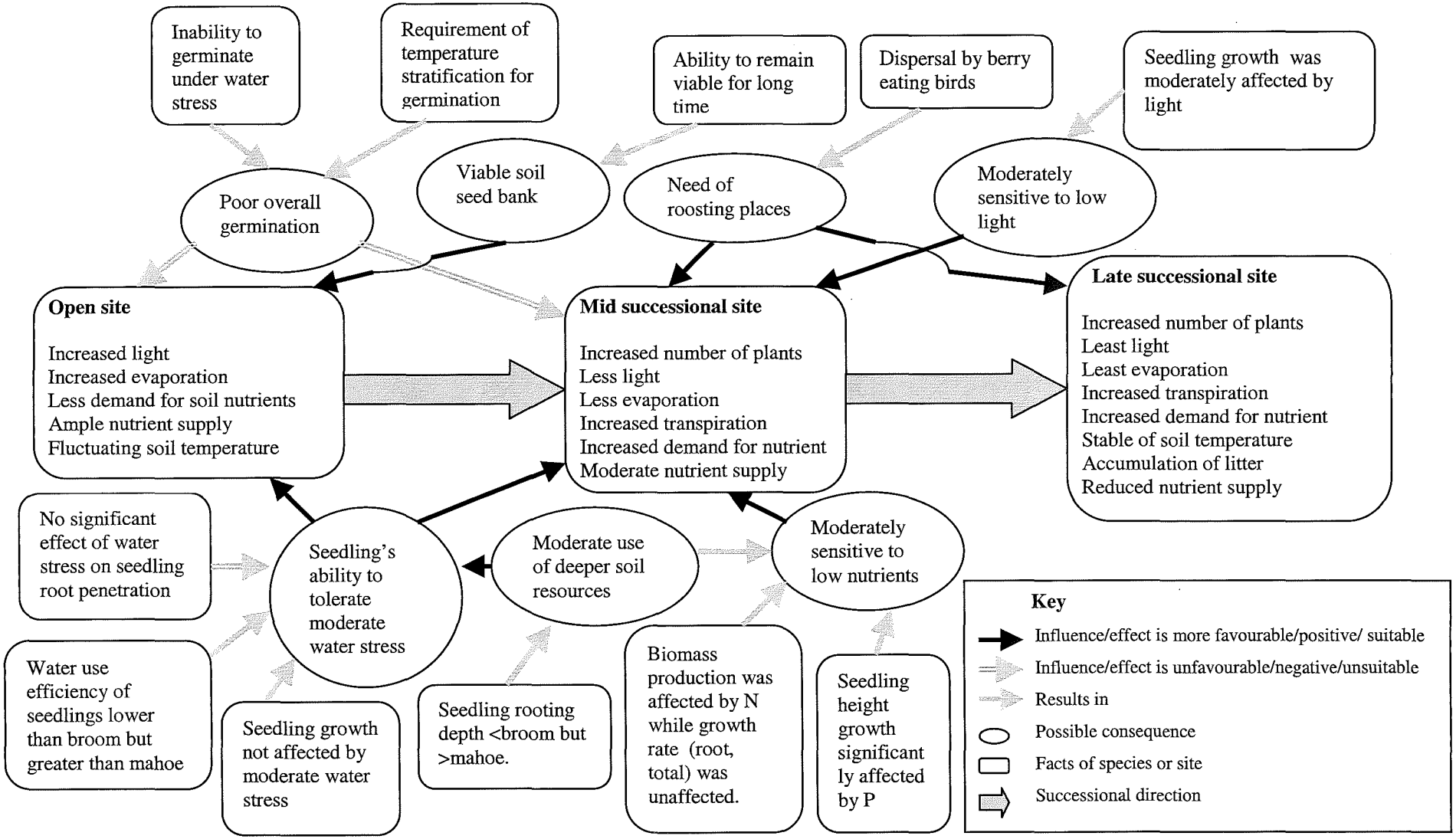


Figure 7.2. Accessing suitability of elder seeds and seedlings to different successional stages

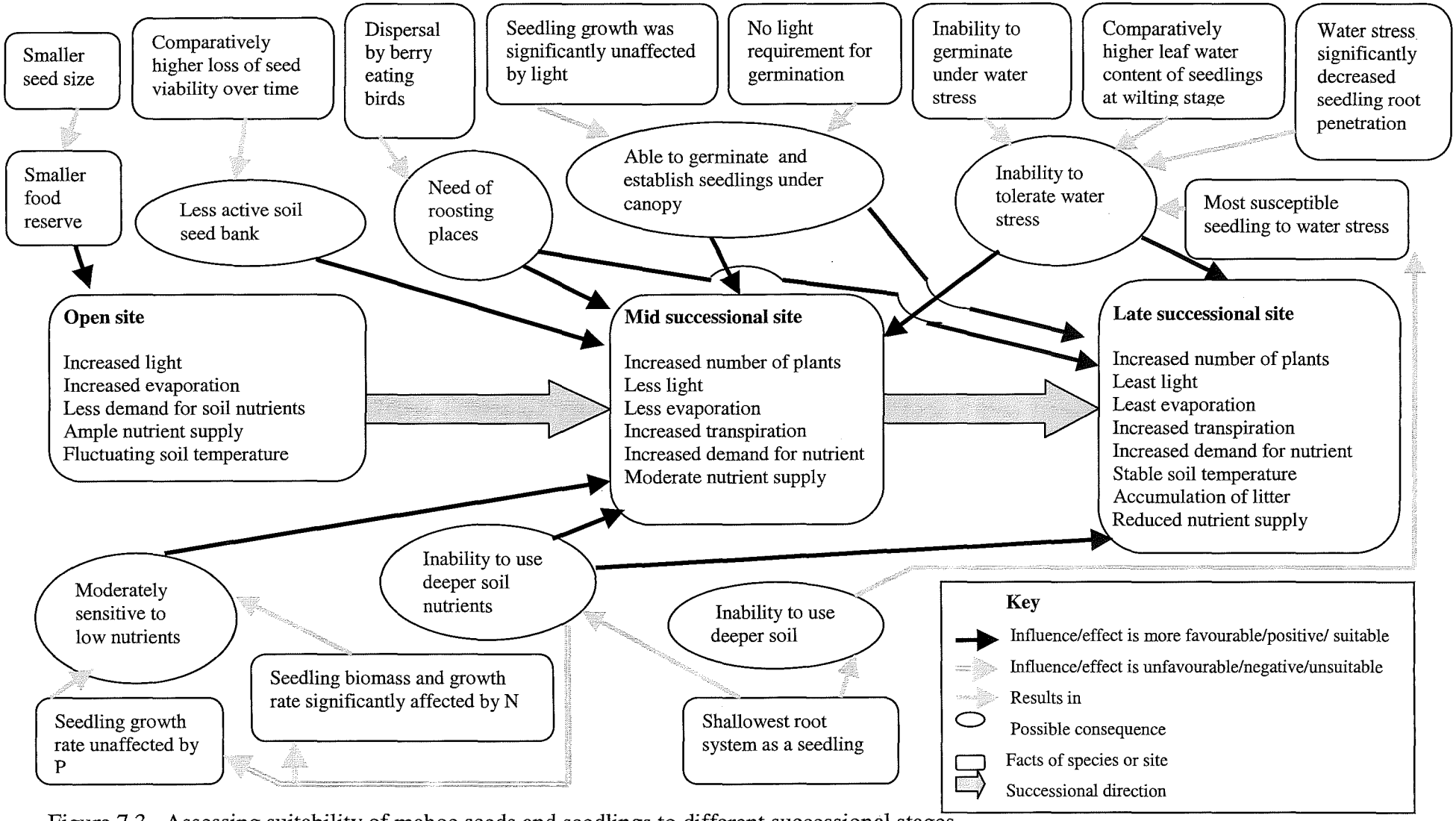


Figure 7.3. Assessing suitability of mahoe seeds and seedlings to different successional stages

7.4. Response ranking of species

Species responses, in terms of differences in their performance in different experiments are summarized in this section by ranking them on a 1-3 scale. This ranking considers performance of a species to be successful in an open, secondary successional site. The higher ranking means that the species response to the effect of treatments is more favourable for an open site. This ranking considers seed characteristics, water requirements and light experiment 1 only, because of the difficulty of singling out specific effects in the light and nutrient trial. In seed characteristics, some attributes where only two species were involved are also not considered, as they would affect the overall ranking. When the differences were not significantly different between species, same ranking was given.

Broom had the highest overall ranking in seed characteristics, light and water requirements showing its suitability for an open secondary succsessioanl site over elder and mahoe. However, mahoe was ranked just below broom in seed characteristics, showing its ability to succeed in open sites provided safe arrival and other factors crucial for establishment are met. Rankings for elder and mahoe were quite similar for light and water requirements (Table 7.2 and 7.3), that suggest their ability to grow in similar environmental conditions. Response ranking does provide a clear indication of broom's suitability of its' position in the studied successional sequence in terms of all tested variables. However, explanation for the successional positions of elder and mahoe was difficult as they both had comparable responses.

Table 7.1. Response ranking in relation to seed characteristics of broom, elder and mahoe.

Variable	Response Ranking		
	1	2	3
Seed Weight	B	E	M
Viability	E	M	B
Scarification	E	M	B
Emerging depth	E	M	B
Total	**B=10** **M=9** **E=5**		

Table 7.2. Response ranking in relation to light requirement of broom, elder and mahoe.

Variable	Response Ranking		
	1	2	3
Experiment 1			
Biomass (root)	E =2	M=2	B
Biomass (shoot)	M=2	E=2	B
Biomass (total)	E =2	M=2	B
R/S ratio	M=1	E=1	B=1
Height	E	M	B
RGR (root)	E =2	M=2	B
RGR (shoot)	M=2	E=2	B
RGR (total)	E =2	M=2	B
Total	**B=22** **M=15** **E=14**		

Table 7.3. Response ranking in relation to water requirements of broom, elder and mahoe.

Variable	Response Ranking		
	1	2	3
Biomass (root)	E	M	B
Biomass (shoot)	M	E	B
Bionass (total)	E	M	B
R/S ratio	M=1	E=1	B=1
Height	M	E	B
RGR (root)	E	M	B
RGR (shoot)	E	M	B
RGR (total)	E	M	B
RWC	M	E	B
Rooting depth	M	E	B
Germ. under stress	E	M	B
WUI	M	E	B
Total	**B=36** **E=18** **M=17**		

7.5. Contribution

This study contributed to the understanding of successional dynamics through:

- An enhanced knowledge of the seed characteristics, light, nutrients and water requirements of broom, elder and mahoe; bridging the need for precise measurements of the three plant species that cannot be measured under field conditions due to the large number of species and effects from numerous environmental factors.

- A provision of supporting evidence for seed characteristics, light, nutrient and water requirements in the species sequence from broom through elder to mahoe postulated by Williams (1983).

- The findings of this research could provide beneficial suggestions for modification or direction of successional management activities. Successful succession management requires designed disturbance, controlled colonization, and controlled species performance Luken (1990). The latter two components could be successfully implemented only with a detailed understanding of the species involved, because controlled colonization includes an increase or decrease in the availability and establishment of species and controlled species performance includes an increase or decrease in the growth and reproduction of plant species. The research findings on the relative resource requirements of broom, elder and mahoe are suggested to be important for the colonization management and performance of species in order to direct succession towards the desired pathways, particularly in the Hoon Hay Valley.

7.6. Recommendations

This study represented a research project that has been undertaken in laboratory/ glass house conditions. Laboratory/ glasshouse based studies are considered to have a greater precision over field experiments (Gibson *et al.* 1999). But Cousens (2000) raised concerns over accuracy of laboratory experiments (due to small sample size, variations in conditions) than carefully managed field experiments. However, experiments under controlled conditions are definitely helpful in determining the effects of single or a small number of factors, but field experimentation is an essential recommendation in order to make real conclusions.

This study tested the species at the seedling stage. Ecological responses of species in the seedling phase might differ to those in their established phase. The differences in the competitive abilities of species dependent on their physiological age, coupled with the uneven age structure of plant communities (Grubb 1977) even though the seedling stage is regarded as most crucial. The outcome of the competition depends on which development stage of one species is pitted against which stage of the other competitor. Therefore field experimentation for both seedling and other developmental stages can be recommended.

The selection of the correct species is essential in achieving successful restoration where such species facilitate and accelerate early stages of the process (Norton 1991; McClanahan and Wolfe 1993). The selection of favourable species is enhanced through the investigation and identification of patterns and processes in vegetation recovery under natural recovery sites similar to the sites intended for restoration (Jorden *et al.* 1987; Norton 1991). The study found that both broom and elder have features that facilitate and accelerate the arrival of native species. Broom plays an important and difficult role in the transformation of a site to a state which becomes

suitable for a wider range of plants. Broom is capable of dominating the vegetation for approximately 15 years before growth is suppressed whereas other early succesional species such as gorse live up to 30 years (Williams 1983). Fast growing broom alters the site to favour other species by i) reducing light intensity to a favorable level and still allowing sufficient light to penetrate through their leafless branches to reach seedlings of the next species in the succession, ii) providing twiggy branches as roosting posts for birds, facilitating the arrival of native berry-bearing species and, iii) enhancing soil resources (nutrients and moisture). Similarly, elder facilitates the site conditions suitable for the next arrival of species such as mahoe. High species diversity under broom canopies highlights the encouragement offered to a large number of species (Voyce 1998). The rapid growth rate and spread of vegetation lead to conditions to which native species are quickly attracted (Williams 1983). Adventive birds play a crucial role in the dissemination of indigenous fruiting plants (e.g. mahoe) as they tend to feed on both indigenous and adventive fruits (Williams and Karl 1996). However, the longevity of elder would hinder the rate of succession as elder is able to live up to 100 years (Molisch 1938) therefore suppressing the development of later arrivals. In addition, longevity is associated with height and later arrivals take a long time to overtop the species establish earlier. Although both broom and elder are important species in facilitating succession and can be recommended, some concerns are raised over the longevity of elder, and as a result the rate of succession may be slowed. Further research could investigate the effect of the selective clearing of elder trees to facilitate mahoe establishment.

References

Aarsen, L.W and Turkington, R., 1985. Within-species diversity in natural populations of *Holcus lanatus, Lolium perenne* and *Trifolium repens* from four different-aged pastures. *Journal of Ecology*, 73: 869-886.

Abdallah, M.M.F., Jones, R.A., El-Beltagy, A.S., 1989. An efficient method to overcome seed dormancy in Scotish broom *(Cytisus scoparious). Environmental and Experimental Botany,* 29: 499-505.

Anon, 1987. *Growing native plants from seed.* Conservation New Zealand pamphlet.

Armstrong, R.A., Mc Gehee. R., 1980. Competitive exclusion. *American Naturalist,* 115:151-170.

Atkinson, I.A.E., 1988. Presidential address: Opportunities for ecological restoration, *New Zealand Journal of Ecology,* 11: 1-12.

Atkinson, I.A.E., 1990. Ecological restoration on islands: prerequisites for success. *In* Towns, D.R., Daugherty, C.H., and Atkinson, I.A.E. (Eds.), *Ecological Restoration of New Zealand Islands, Conservation Sciences Publication,* Department of Conservation, Wellington. No.2: 166-170.

Aronson, J., Floret, C., Le Flo'ch, E., Ovalle, C., Pontanier, R., 1993. Restoration and rehabilitation of degraded ecosystems in arid and semi arid lands. *Restoration ecology*, 6: 8-17.

Augspurger, C.K., 1984. Light requirements of neotropical tree species: a comparative study of growth and survival. *Journal of Ecology*. 72:777-795.

Bakker, J.P., Bakker, E.S., Rosen, E., Verweij, G.L., Bekker,R.M., 1996. Soil seed bank composition along a gradient from dry alvar grassland to Juniperus shrub land. *Journal of Vegetation Science*, 7:165-176.

Bannister, P., 1986. Observations on water potential and drought resistance of trees and shrubs after a period of summer drought around Dunedin. New Zealand *New Zealand Journal of Botany*, 24: 387-392.

Baskin, J.M and Baskin, C.C., 1979. Promotion of germination of *Stellaria media* seeds by light from green safe lamp. *New Phytol.* 82: 381-383.

Baskin, C.C and Baskin, J.M., 1998. *Seeds: ecology, biogeography and evolution of dormancy and germination.* Academic Press, London. 666p.

Bazzaz, F.A., 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. *In* Mooney, H.A. and Godron, M. (Eds.) *Disturbance and Ecosystems*, Springer-Verlag, New York, USA. 259-275pp.

Bazzaz, F.A., 1987. Experimental studies on the evolution of niche in successional plant populations. *In* Gray, A.J., Crawley, M.J., Edwards, P.J (Eds.) *Colonization, Succession and stability: 26 th Symposium of the British Ecological Society,* Blackwell Scientific, London. 245- 272pp.

Bazzaz, F.A., 1990. Plant-plant interactions in successtional environments. *In* Grace, J.B and Tilman, D (Eds.) *Perspectives on plant competition.* Academic Press, London. 239-263pp.

Beeby, A., 1993. *Applying Ecology*. Chapman & Hall, London, 441p.

Bellingham, M., 1990. Public involvement in island restoration. *In* Towns, D.R., Daugherty, C.H., and Atkinson, I.A.E. (Eds.) *Ecological restoration of New Zealand Islands, Conservation Sciences Publication,* Department of Conservation, Wellington, No.2: 166-169pp.

Bennett, O.L and Doss, B.D., 1960. Effect of soil moisture level on root distribution of cool season forage species. *Agronomy Journal*, 52: 204-207.

Black, C.H and Marion, G.M., 1984. Phosphorus availability across a southern California chaparral fire cycle chronosequence. *Bulletin of the Ecological Society of America*, 65:271.

Bormann, F.H and Likens, G.E., 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist*, 67: 660-669.

Bossard, C.C., 1993. Seed germination in the exotic shrub *Cytisus Scoparious* (Scotish broom) in California. *Madrono.* 40: 47-61.

Bradbeer, J.W., 1988. *Seed dormancy and germination.* Chapman and Hall, Glassgow, 146p.

Bradford, K.J and Hsiao, T.C., 1982. Physiological responses to moderate water stress. *In* Lange. O.L., Nobel, P.S., Osmond, C.B., Ziegler, H (Eds.) *Encyclopedia of Plant Physiology.* Springer-Verlag, Berlin, 263-324pp.

Bradshaw. A.D., 1983. The reconstruction of ecosystems. *Journal of Applied Ecology*, 20:1-17.

Bradshaw. A.D., 1984. Ecological principles and land reclamation practice, *Landscape Planning,* 11: 35-48.

Bradshaw, A.D., 1987a. Restoration: an acid test for ecology. *In* Jordan III, W.R., Gilpin, M.E., Aber, J.D., (Eds.), *Restoration ecology: A synthetic approach to ecological research.* Cambridge University Press, Cambridge, 23-29pp.

Bradshaw, A.D., 1987b. The reclamation of derelict land and the ecology of ecosystems. *In* Jordan, W.R.III., Gilpin, M.E., Aber, J.D., (Eds.). *Restoration ecology: A synthetic approach to ecological research.* Cambridge University Press, Cambridge, 53-74pp.

Bradshaw, A.D and Chadwick, M.J., 1980. The restoration of land: the ecology and reclamation of derelict and degraded land. Blackwell Scientific, Oxford. 317p.

Brenner, F.J., and Kelly, J., 1981. Characteristics of bird communities on surface mine lands in Pennsylvania. *Environmental Ethics,* 5: 441-449.

Brown, A.H.F and Costerhuis. L., 1981. The role of buried seed in copicewoods. *Biological Conservation*, 21:19-38.

Browse, P.D.A.M., 1979. *Hardy, woody plants from seeds.* Growers books, London, 163p.

Burrows, C.J., 1990. *Processes of vegetation change*. Unwin-Hyman, London, 551p.

Burrows, C.J., 1993. Germination requirements of seeds of native trees, shrubs and wines. *Canterbury Botanical Society Journal*, 27: 42-46.

Burrows, C.J., 1994a. Fruit, seeds, birds and the forests of Banks Peninsula. *New Zealand Journal of Natural Sciences*, 21:87-107.

Burrows, C.J., 1994b. Seed trapping in the Ahuriri Summit Bush Scenic Reserve, Port Hills, Western Banks Peninsula, 1985-1986. *New Zealand Journal of Botany*, 32:183-206.

Burrows, C.J., 1994c. Fruit types and seed dispersal modes of woody plants in Ahuriri Summit Bush Port Hills, Western Banks Peninsula, Canterbury, New Zealand. *New Zealand Journal of Botany,* 32:169-181.

Burrows, C.J., 1995a. Germination behavior of seeds of the New Zealand species *Fuchsia excorticata, Griselinia littoralis, Macropiper excelsum,* and *Melicytus ramiflorus. New Zealand Journal of Botany,* 33: 131-140.

Burrows, C.J., 1995b. Germination behavior of seeds of the New Zealand species *Aristotelia serrata, Coprosma robusta, Cordyline australis, Myrtus obcordata* and *Schefflera digitata. New Zealand Journal of Botany,* 33: 257-264.

Burrows, C.J., 1995c. Germination behavior of seeds of six New Zealand woody plant species. *New Zealand Journal of Botany,* 33: 365-377.

Burrows, C.J., 1996a. Radiocarbon dates for Holocene fires and associated events, Canterbury, New Zealand. *New Zealand Journal of Botany,* 34: 111-121.

Burrows, C.J., 1996b. Germination behavior of seeds of seven New Zealand vine plant species. *New Zealand Journal of Botany,* 34: 93-102.

Burrows, C.J., 1996c. Germination behavior of seeds of the New Zealand woody species *Melicope simplex, Myoporum laetum, Myrsine divaricata,* and *Urtica ferox. New Zealand Journal of Botany,* 34: 205-213.

Cairns, J., 1989. Restoring damaged ecosystems: is pre-disturbance condition a viable option? *The Environmental Professional,* 11: 152-159.

Canham, C.D., 1985. Suppression and release during canopy recruitment in *Acer saccharum. Bulletin of the Torrey Botanical Club*, 112: 134-145.

Case, T.J., 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of National Academy of Science*, USA, 87: 9610-9614.

Catsky, J., 1974. Direct methods for water content determination. *In* Slavik, B (Ed.) *Methods of studying plant water relations.* Chapman and Hall, London. 121-156pp.

Chapin, F.S., 1980. The mineral nutrition of wild plants. Annu. Rev.Ecol. Syst, 11: 233-260.

Cheke. A.S., Weerachai. N., Yankoses. C., 1979. Dormancy and dispersal of secondary forest species under the canopy of primary tropical rain forest in northern Thailand. *Biotropica,* 11: 88-95.

Chester, P.I and Raine, J.I., 1990. Mana island revegetation: Data from late Holocene pollen analysis. *In* Towns, D.R., Daugherty, C.H., Atkinson, I.A.E. (Eds.), *Ecological restoration of New Zealand Islands. Conservation Sciences Publication,* Department of Conservation, Wellington, No.2: 113-122pp.

Clarkson, D.T and Hanson, J.B., 1980. The mineral nutrition of higher plants. *Annual Review of Plant physiology,* 31: 239-298.

Clements, F.E., 1916. *Plant succession: an analysis of the development of vegetation.* Carnegie Institute, Washington. 512p.

Colinvaux, P.A., 1986. *Ecology.* John Wiley & Sons, New York, 725p.

Connell, J.H and Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist,* 111: 1119-1144.

Cooper, W.S., 1913. The climax forest of Lsle Royale, Lake Superior and its development. *Botanical Gazette*, 55:1-44.

Coulter, J.D., 1975. The climate. *In* Kuschel, G (Ed) *Biogeography and ecology in New Zealand.* Dr W.Junk b.v. Publishers, The Hage, 87-138pp.

Cousens, R., 2000. Greenhouse studies of interactions between plants: the flaws are in interpretation rather than design. *Journal of ecology,* 88:352-353.

Cowles, H.C., 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette.* 27: 95-117.

Crawford, R.M.M., 1989. *Studies in plant survival.* Blackwell Scientific Publications, London, 296p.

Cullen, N.J., 1996. *Surface-atmosphere interactions over regenerating indigenous vegetation, Hoon Hay Valley, Port Hills, Canterbury.* MSc thesis, University of Canterbury, 120p.

Culley, J.L.B., 1993. Density and compressibility. *In* Carter, M.R. (Ed.) *Soil sampling and methods of analysis.* Canadian society of soil science, Lewis Publ, 529-539pp.

Daily, G.C., 1993. Social constraints on restoration ecology. *In* Saunders, D.A., Hobbs, R,J., Ehrlich, P.R., (Eds.) *Reconstruction of fragmented ecosystems: Nature Conservation.* Surrey Beatty & Sons, Chipping Norton, NSW. 3:9-16pp.

Dale.V.H., 1989. Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche. *Canadian Journal of Botany*, 67: 1434-1441.

Daugherty, C.H., Towns, D.R., Atkinson, I.A.E., Gibbs, G.W., 1990. The significance of biological resources of New Zealand for ecological restoration. *In* Towns, D.R., Daugherty, C.H., Atkinson, I.A.E. (Eds.) *Ecological restoration of New Zealand islands. Conservation Sciences publication,* Department of conservation, Wellington, No.2: 3-8pp.

Dawson. J and Lucas. R. 1993. *Lifestyles of New Zealand forest plants.* Victoria University Press. Wellington, 176p.

Del Moral, R. and Wood, D.M., 1988. Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA after a volcanic eruption. *Vegetatio,* 74: 11-27.

Del Moral, R., Titus, J.H., Cook, A.M., 1995. Early primary succession on Mount Helens, Washington, USA. *Journal of Vegetation science*, 6:107-120.

Diamond, J.M., 1986. The design of the nature reserve system for Indonesia. *In* Soul'e, M.E (Ed.) *Conservation Biology: The science of scarcity and diversity*. Sinauer, Sunderland, MA. 485-503pp.

Dias-Filho, M.B and Dawson, T.E., 1995. Physiological responses to soil moisture stress in two Amazonian gap invader species. *Functional Ecology,* 9: 213-221.

Druce, A.P., 1957. Botanical survey of an experimental catchment, Taita, New Zealand. *New Zealand Department of Scientific and Industrial Research Bulletin,* 24.

Drury, W.H and Nisbet,I.C.T., 1973. Succession. *Journal of the Arnold Arboretum,* 54: 331-368.

Dubos, R., 1976. Symbiosis between the earth and mankind. *Science.* 193: 462-472.

Dungan, R.J., 1997. *Spatial coupling of plant recruitment processes; vegetation change and the regeneration ecology of Hoon Hay Valley, Port Hills, Canterbury, New Zealand.* Unpublished MSc. thesis, University of Canterbury, Christchurch, New Zealand, 110p.

Egler, F.E., 1954. Vegetation science concepts 1. Initial floristic composition: a factor in old-field vegetation development. *Vegetatio*, 4: 412-417.

Elliot, R., 1994. Extinction, Restoration, Naturalness. *Environmental Ethics,* 16: 135-144.

Enright, N.J and Cameron, E., 1988. The soil seed bank of a kauri *(Agathis australis)* forest remnant Auckland. *New Zealand Journal of Botany,* 26:223-236.

Etherington, J.R., 1993. Germination and soil water potential. *In* Hendry, G.A.F., and Grime, J.P. (Eds.) *Methods in comparative plant ecology: a laboratory manual.* Chapman and Hall, London, 190-192pp.

Evans, R.D and Ehleringer, J.R., 1994. Water and Nitrogen dynamics in an arid woodland. *Oecologia*, 99: 233-242.

Ewel, J.J., 1987. Restoration is the ultimate test of ecological theory. *In* Jordan III, W.R., Gilpin, M.E., Aber, J.D., (Eds.) *Restoration ecology: A synthetic approach to ecological research.* Cambridge University Press, Cambridge, 31-33pp.

Fagerstrom, T., 1989. Lotteries in communities of sessile organisms. *Trends in Ecology and Evolution.* 3: 303-306.

Fenner, M., 1978. A comparison of the abilities of colonizers and closed turf species to establish from seed in artificial swards. *Journal of Ecology*, 66: 953-965.

Fenner, M., 1983. Relationship between seed weight, ash content and seedling growth in twenty-four species of Compositae. *New Phytologist*, 95: 697-706.

Fenner, M., 1985. *Seed Ecology.* Chapman and Hall Ltd, London, 151p.

Fenner, M., 1987. Seed characteristics in relation to succession. *In* Gray, A.J., Crawley, M.J., Edwards, P.J (Eds.) *Colonization, succession and stability*: The 26 th symposium of the British Ecological Society. Balckwell Sciecntifc Publications, London, 103-114pp.

Fenner, M., 1992. *Seeds: The ecology of regeneration in plant communities.* C.A.B. international, Wallingford, Oxon, 373p.

Fitter, A.H. and Hay, R.K.M., 1981. *Environmental physiology of plants.* Academic Press Inc , London. 355p.

Fitzgerald, O., 1966. Soils of Heathcote County, Canterbury, New Zealand. *New Zealand DSIR Soil Bureau Report* 1:1-33pp.

Fullager, P.J., 1978. *Report on the rabbits on Phillip Island, Norfolk Island.* Division of wildlife research, CSIRO, Lyneham, A.C.T. 2602.

Gibson, D.J., Connolly, J., Weidenhamer, J.D., 1999. Designs for greenhouse studies of interaction between plants. *Journal of ecology,* 87: 1-16.

Gleason.H.A., 1917. The structure and the development of the plant association. *Bulletin of the Torrey Botanical Club,* 43: 463-481.

Gleason, H.A., 1927. Further views on the succession-concept. *Ecology.* 8: 299-326.

Griffiths, E., 1974. Soils of part of the Port Hills and adjacent plains, Canterbury, New Zealand. *DSIR Soil Bureau Bulletin,* 35.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111: 1169-1194.

Grime, J.P., 1979. *Plant strategies and vegetation process.* John Wiley &Ssons, Chichester. 222p.

Grime, J.P., 1987. Dominant and subordinate components of plant communities: implications for succession, stability and diversity. *In* Gray, A.J., Crawley, M.J., Edwards, P.J. (Eds.) *Colonization, succession and stability*, Blackwell Scientific Publications, Oxford. 103-115 pp.

Grime, J.P., Mason, G., Curtis, .A.V., Rodman, J., Band, S.R., Mowforth, M.A., Beal, A.M., Show, S., 1981. A comparative study of germinating characteristics in a local flora. *Journal of Ecology*, 69: 1017-1059.

Gross, K.L., 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology*, 72: 369-387.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, 52: 107-145.

Gunn, A.S., 1991. The restoration of species and natural environments. *Environmental Ethics,* 13: 291-310.

Hall, J.B and Swaine, M.D., 1980. Seed stocks in Ghanaian forest soils. *Biotropica,* 12: 256-263.

Halpern, C.B., Frenzen, P.M., Means, J.E., Franklin, J.F., 1990. Plant succession in areas of scorched and blown down forest after the 1980 eruption on Mount St. Helens, Washington. *Journal of Vegetation Science*, 1: 181-194.

Harcombe, P.A., 1977. The influence of fertilizers on some aspects of succession in a humid tropical forest. *Ecology,* 58: 1375-1383.

Harper, J.L., 1977. *Population biology of plants.* Academic Press, London, 892p.

Harper, J.L., Clatworthy, J.N., McNaughton, I.H., Sagar, G.R., 1961. The evolution and ecology of closely related species living in the same area. *Evolution,* 15: 209-227.

Hart, J.W., 1988. *Light and Plant growth.* Unwin Hyman, London. 204p.

Hellmers, H., Horton, J.S., Juhren, G., O'Keefe, J., 1955. Root systems of some chaparral plants in Sourthern California. *Ecology*, 36: 667-678.

Hermes, N., Greenwood, D., Hinchey, M., 1986. Eradication of rabbits from Phillip Island. *Australian Ranger Bulletin*, 4: 34-37.

Hewitt, A.E., 1993. *New Zealand soil classification.* Landcare research science series no.1, Landcare research New Zealand, 133p

Hills, M.H and Vankat, J.L., 1982. Species removal from a first-year old-field plant community. *Ecology,* 63: 705-711.

Hobbs, R.J., 1992. Corridors for conservation: Solution or bandwagon? *Treands in Ecology and Evolution,* 7: 389-392.

Hobbs, R.J., 1993. Can re-vegetation assist in the conservation of biodiversity in agricultural areas? *Pacific Conservation Biology,* 1:29-38.

Hobbs, R.J and Norton, D.A., 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology*, 4: 93-110.

Horn, H.S., 1971. *The adaptive geometry of trees.* Princeton, Princeton University Press.

Horn, H.S., 1976. Succession. *In* May. R.M. (Ed.) *Theoretical ecology. Principles and applications.* W.B. Saunders, Philadelphia. 187-204pp.

Hsiao, T.C., 1973. Plant responses to water stress. *Annual Review Plant Physiology*, 24: 519-570.

Hsu, S.B., Hubbell, S.P., Waltman, P., 1977. A mathematical thoery for single nutrient competition in continuous cultures of micro-organisms. *SIAM Journal of Applied Mathematics,* 32: 366-383.

Hunt, 1982. *Plant growth curves: The functional approach to plant growth analysis.* Edward Arnold, London. 248p.

Ingestad, T and Lund, A.B., 1979. Nitrogen stress in birch seedlings. Growth techniques and growth. *Physiol. Plant.* 45: 137-148.

Innes, K.P and Kelly, D., 1992. Water potentials in native woody vegetation during and after a drought in canterbury. *New Zealand Journal of Botany*, 30: 81-94.

Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M.A., Zinnel, K.C., 1987. Old field succession on a Minnesota sand plain. *Ecology*. 68: 12-26.

Jane, G.T and Green, T.G.A., 1986. Etiology of forest dieback areas within the Kaimai Range, North Island, New Zealand. *New Zealand Journal of Botany*, 24: 513-527.

Janzen, D.H., 1986. *Guanacaste National Park: Tropical ecological and cultural restoration.* Editorial Universidad Estatal a Distancia, San Jose, Coata Rica.

Jayet, D.F., 1986. *An examination of observed climatic trends/changes over Banks Peninsula and the surrounding plains and their synoptic climatology.* MSc thesis University of Canterbury, 246p.

Jimenez, H. E and Armesto, J.J., 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. *Journal of Vegetation Science*, 3: 579-586.

Jones, M.M., Turner, N.C., Osmond, C.B., 1981. Mechanisms of drought resistance. *In* Paleg, L.P. and Aspindall, D (Eds.) *The physiology and biochemistry of drought resistance in plants,* Academic Press, New York. 15-37pp.

Jones, H.G., 1993. Drought tolerance and water use efficiency. *In* Smith, J.A.C and Griffiths, H (Eds.), *Water deficits*, BIOS Scientific Publishers Ltd. Oxford. UK. 193-203pp.

Jordan, W.R., Gilpin, M.E., Ader, J..D. (Eds.) 1987. *Restoration ecology: A synthetic approach to ecological research*, Cambridge University Press, Cambridge, 342p.

Kaufmann, M.R., 1968. Water relations of pine seedlings in relation to root and shoot growth. *Plant plysiology*. 43: 281-288.

Keddy, P.A., Wisheu, I.C., Shipley, B., Gaudet, C., 1989. Seed bank and vegetation management for conservatio: towards predictive community ecology. *In* Leck, M.A., Parker, V.T., Simpson, R.L (Eds.), *Ecology of Soil Seed Banks.* Academic press, San Diego, 347-363pp.

Kozlowski, T.T., Kramer, P.J., Parlardy, S.G., 1991. *The physiological ecology of woody plants,* Academic Press, 657p.

Kramer, P.J., 1969. *Plant and soil water relations*. McGraw-Hill, New York, 347p.

Kramer, P.J., 1983. *Water ralations of plants.* Academic Press, New York. 489p.

Kramer, P.J and Boyer, J.S., 1995. *Water relations of plants and soils.* Academic Press, London, 95p.

Kuhn, T. S., 1970. *The structure of scientific revolutions.* Second edition, University Press, Chicago, Illinois, USA, 210p.

Lamont, B., 1999. Pressure-volume curves. *In* Atwell, B.J., Kriedemann, P.E., Turnbull, C.G.N. (Eds.) *Plants in action: Adaptation in nature, performance in cultivation.* 465-467pp.

Lawton, J.H., 1987. Are there assembly rules for successional communities? *In* Gray, A.J., Crawley, M.J., and Edwards, P.J. (Eds.) *Colonisation, succession and stability*, Blackwell, Oxford. 225-244pp.

Leishman, M.R and Westoby, M., 1994. The role of large seed size in shaded conditions: experimental evidence. *Functional ecology,* 8:205-214.

Ludlow, M.M., 1987. Defining shoot water status in the most meaningful way to relate to physiological processes. *Proceedings of international conference on measurement of soil and plant water status.* Utah State University, 47-53pp.

Luken, J. O., 1990. *Directing ecological succesion.* Chapman and Hall, London. 251p.

Mackey, D.B., 1972. The measurment of viability. *In* Roberts, E.H. (Ed.) *Viability of seeds*, Chapman and Hall Ltd, London. 173-207pp.

Magnuson, J.J., Regier, H.A., Christie, W,J., Sonzogni, W.C., 1980. To rehabilitate and restore Great Lakes ecosystems. *In* Cairns, J.J (Ed.) *The recovery process in damaged ecosystems,* Ann Arbor science publishers, Inc., Ann Arbor, Michigan, 95-112 pp.

Mansfield, B., 1996. Moving from successful restoration of islands to ecosystem restoration on mainland, New Zealand. Paper presented at IUCN world conservation congress.

Matson, P.A and Boone, R.D., 1984. Natural disturbance and nitrogen mineralisation:wave-form dieback of mountain hemlock in the Oregon Cascades. *Ecology,* 65: 1511-1516.

Matson, P.A and Vitousek, P.M., 1981. Nitrification potentials following clear cutting in the Hoosier National forest, Indiana. *Forest Science*, 27: 781-791.

McClaren, R.G and Cameron, K.C., 1990. *Soil science: An introduction to the properties and management of New Zealand soils.* Oxford University Press, Auckland, 294p.

McClanahan, T.R and Wolfe, R.W., 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology*, 7: 279-288.

McIntosh, R.P., 1980. The relationship between succession and the recovery process in ecosystems. *In* Cairns, J. (Ed.) *The recovery process in damaged ecosystems.* Ann Arbor Science Publishers, Ann Arbor, 11-62pp.

Merton, D.V., 1972. Cuvier- an island restored. *Forest and Bird*, 184: 7-9.

Meurk, C.D., 1993. *Botanical survey and land use management of the A.F Scott Estate, Hoon Hay Valley, Port Hills.* Landcare Research Ltd. Contract report LC9394/44.

Miller, H.G., 1981. Forest fertilization: some guiding concepts. *Forestry*, 54: 157-167.

Miles, J., 1987. Vegetation succession: Past and present perceptions. *In* Gray, A.J., Crawley, M.J., Edwards, P.J (Eds.) *Colonization, Succession and stability: 26 th Symposium of the British Ecological Society,* Blackwell Scientific Publications, London. 1-29pp.

Milton, W.E.J., 1939. Occurrence of buried viable seeds in soils at different elevations on a salt marsh. *Journal of Ecology*, 27: 149-159.

Miyawaki, A., 1992. Restoration of evergreen broad-leaved forests in the Pacific region. *In* Wali, M.K. (Ed.) *Ecosystem rehabilitation: ecosystem analysis and synthesis.* SPB Academic publishers, The Hague, The Netherlands, 2: 233-245pp.

Molisch, H., 1938. *The longevity of plants. Science Press.* Pennsylvania. 226p.

Molloy, B.J.P., 1969. Recent changes of the vegetation. *In* Knox. G.A. (Ed.) *The natural history of Canterbury.* A.H. and A.W. Reed Pub. Wellington. 340-460pp.

Molloy, B.J.P., Burrows, C.J., Cox, J.E., Johnson, J.A., Wardle, P., 1963. Distribution of subfossil remains, Eastern South Island, New Zealand. *New Zealand Journal of Botany.* 1: 68-77.

Molyneux, D.E and Davis, W.J., 1983. Rooting pattern and water relations of three pasture grasses growing in drying soil. *Oecologia,* 58: 220-224.

Moore, R.P., 1972. Tetrazoliun staining for assessing seed quality. *In* Heydecker, W (Ed.) *Seed Ecology.* Butterworths, London, 234-245pp.

Morrison, D., 1987. Landscape restoration in response to previous disturbance. *In* Monica, G.T (Ed.) *Landscape heterogenecity and disturbance.* Springer Verlag, New York, 160p.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution,* 10: 58-62.

Murdoch, A.J and Ellis, R.H., 1992. Longivity, Viability and Dormancy. *In* Fenner, M. (Ed.) *Seeds: The ecology of regeneration in plant communities.* C.A.B. International, U.K, 193-229pp.

Nakashizuka, T., Iida, S., Suzuki, W., Tanimoto, T., 1993. Seed dispersal and vegetation development on a debris avalanche on the Ontake volcano, central Japan. *Journal of Vegetation Science*, 4: 537-542.

Nguyen, A and Lamant, A., 1989. Variation in growth and osmatic regulation of roots of water- stressed maritime pine (*Pinus pinaster*) provenances. *Tree Physiology*, 5: 123-133.

Noble, I.R and Slatyer, R.O., 1978. The effect of disturbance on plant succession. *Proceedings of the ecological society of Australia,* 10: 135-145.

Norton, D.A., 1991. *Restoration of indigenous vegetation on sites disturbed by alluvial gold mining in Westland.* Resource allocation report 3, Energy and Resource Division, Ministry of Commerce, Wellington.

Norton, D.A., 1993. Mainland habitat islands: *A vision for New Zealand nature conservation.* West coast conservatory technical report series No.2 Department of Conservation, Hokitika, New Zealand.

Norton, D.A., 1994. *Ecological retoration, Conservation management.* Lecture notes, University of Canterbury, New Zealand.

Norton, D.A., 1995. *The Hoon Hay Valley Restoration ecology research programme- a discussion document.* University of Canterbury, New Zealand.

O'Brien, W.J., 1974. The dynamics of nutrient limitation of phytoplankton algae: a model reconsidered. *Ecology*, 50: 930-938.

O'Cain, M., 1997. *The role of possums in forest regeneration, Hoon Hay Valley, Port Hils, Canterbury.* MSc. Thesis, University of Canterbury, 139p.

Odum, E.P., 1969. The strategy of ecosystem development. *Science,* 164: 262-270.

Oertli, J.J., 1976. The status of water in the plant: Theoretical consideration. *In* Lange, O.L., Kappen, L., Schub, E.D (Eds.) *Water and plants: Problems and modern approaches,* Springer-Verlag, New York.

Ogilvie, G.B., 1978. *The Port Hills of Christchurch.* A.H. and A.W. Reed Publications Wellington, 246p.

Olff, H., Pegtel, D.M., Van Groenendael, J.M., Bakker, J.P., 1994. Germination strategies during grassland succession. *Journal of Ecology*, 82: 69-77pp.

Partridge, T.R., 1989. Soil seed banks of secondary vegetation on the Port Hills and Bank Peninsula, Canterbury, New Zealand and their role in succession. *New Zealand Journal of Botany* 27: 421-436.

Partridge, T.R., 1992. Successional interactions between bracken and broom *(Cytisus scoparius)* on the Port Hills, Canterbury, New Zealand. *Journal of Applied Ecology*, 29: 85-91.

Petrie, L.M., 1963. *From bush to cocksfoot. An essay on the destruction of Banks Peninsula's forests.* Unpublished MSc. thesis. University of Canterbury, Christchurch, New Zealand, 114p.

Pickett, S.T.A., 1976. Succession: an evolutionary explanation. *American Naturalist*, 110: 107-119.

Poole, A.L and Adams, J. N.M., 1990. *Trees and shrubs of New Zealand.* DSIR Publishing, Wellington, 256p.

Prance, G.T., 1991. Rates of loss of biological diversity: a global view. *In* Spellerberg, I.F., Goldsmith, F.B., Morris, M.G., (Eds.) *Scientific management of temperate communities for conservation.* Blackwell, Oxford. 27-44pp.

Primack, R.B., 1979. Reproductive effort in annual and perennial species of *Plantago (Plantaginaceae). American Naturalist*, 114: 51-62.

Rao, P.B., 1988. Effects of environmental factors on germination and seedling growth in *Qiercus floribunda* and *Cupressus torulosa*, tree species of central Himalaya. *Annals of Botany,* 61:531-540.

Rao, P.B. and Singh, S.P., 1985. Response breadths on environmental gradients of germination and seedling growth in two dominat forest tree species of central Himalaya. *Annals of Botany*, 56: 783-794.

Ray, G.J., 1993. *The ecological restoration of a Caribbean dry forest on the island of St. John, U.S Virgin islands.* Ph.D thesis, The University of Wisconsin, 119p.

Reader, R.J., Jalili, A., Grime, J.P., Spencer, R.E., Matthews, N., 1993. Penetration and response to drought. *In* Hendry, G.A.F. and Grime, J.P. (Eds.*) Methods in comparative plant ecology.* Chapman and Hall, London, 173-176pp.

Reay, S.D., 1996. *The success of three restoration plantings at Kennedy's Bush, Port Hills, Canterbury, New Zealand.* MSc. Thesis. University of Canterbury, 128p.

Reay, S.D and Norton, D.A., 1999a. *Phormium tenax*, an unusual nurse plant. *New Zealand Journal of Ecology.* 23: 81-85.

Reay, S.D and Norton, D.A., 1999b. Assessing the success of restoration plantings in a temperate New Zealand forest. *Restoration Ecology.* 7: 298-308.

Roberts, B.R and Schnipke, V.M., 1994. The relative water demand of five urban tree species. *Journal of Arboriculture* 20: 156-159.

Roxburgh, J.R., 1992. *The relationship between light and regeneration ecology of Himalayan Honeysuckle (Leycesteria formosa) and elder (Sambucas nigra) and their distribution.* M.Sc. thesis, University of Canterbury, New Zealand, 119p.

Salisbury, E.J., 1942. *The reproductive capacity of plants.* Studies in quatitative biology, G. Bell and Sons, London, 244p.

Salmon, J.T., 1975. The influence of man on the biota. *In* Kuschell,G. (Ed.) *Biogeography and ecology of New Zealand.* W. Junk Publishers, The Hague.

Salmon, J.T., 1986. *A field guide to the native trees of New Zealand.* Reed Methuen Publishers, Auckland, 228p.

SAS institute Inc., 1995. SAS/STAT Procedures guide, version 6.11, Cary, NC.

Sauser, L.J., 1998. The once and future forest: A guide to forest restoration strategies, Andropogon Associates, Island Press, California, 381p.

Schaller, F.W and Sutton, P. (Eds.) 1978. *Reclamation of drastically disturbed lands.* Madison: American society of agronomy.

Sharp, A., 1956. *Ancient Voyagers to the Pacific.* Polynesian Society No.32, Wellington, 191p.

Sharp, R.E. and Davies, W.J., 1985. Root growth and uptake by maize plants in drying soil. *Journal of Experimental Botany*, 36: 1441-1456.

Sheldon, J.C., 1974. The behavior of seeds in soil. III. The influence of seed morphology and the behavior of seedling on the establishment of plants from surface-lying seeds. *Journal of Ecology*, 62: 47-66.

Silvertown, J.W., 1987. *Introduction to plant population biology.* Longman Scientific and Technical Group. UK. 229p.

Simberloff, D., 1990. Reconstructing the ambiguous: can island ecosystems be restored? *In* Towns, D.R., Daugherty, C.H., and Atkinson, I.A.E. (Eds.) *Ecological restoration of New Zealand islands.* Conservation Sciences publication, Department of Conservation, Wellington.No.2: 37-51pp.

Sinclair, T.R. and Ludlow, M.M., 1985. Who taught plants thermodynamics? The unfulfilled potential of plant water porential. *Australian Journal of Plant Physiology*, 12: 213-217.

Slavik, B., 1974. *Methods of studying plant water relations.* Springer-Verlag, New York. 449p.

Smith, A.J., 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* 56: 19-34.

Smith, J.M.B and Harlen, R.L., 1991. Primary observations on the seed dynamics of broom *(Cytisus scoparius)* at Barrington Tops, New South Wales. *Plant Protection Quarterly*, 6: 73-78.

Sokal, R.R. and Rohlf, E.F., 1981. Biometry. *The principles and practice of statistics in biological research.* Second edition. W.H Freeman and Company. New York, 859p.

Sun, O.J., 1993. *Genetics and physiology of Nothofagus solandri var. cliffortoides and Nothofagus menziesii- A comparative study.* Ph.D thesis, University of Canterbury, New Zealand. 279p.

Sutcliffe, J., 1979. *Plants and water.* The Institute of Biology's Studies in Biology no. 14, First edition, Edward Arnold Publication, London. 81p.

Tagawa, H., Suzuki, E., Partomiharjo, T., Suriadarma, A., 1985. Vegetation and succession on the Krakatau Islands Indonesia. *Vegetatio.* 60: 131-145.

Tansley, A.G., 1939. *The British islands and their vegetation.* Cambridge University Press. 930p.

Teketay, D. and Anders, G., 1995. Soil seed banks in Afromontane forests of Ethiopia. *Journal of Vegetation Science,* 6: 777-786.

Teare, I.D., Kanemasu, E.T., Powers, W.L., Jacobs, B.S., 1973. Water-use efficiency and relation to crop canopy area, stomatal regulation, and root distribution. *Agronomy Journal,* 65: 207-211.

Thompson, K., 1993. Persistence in soil. *In* Hendry, G.A.F and Grime, J.P (Eds.) *Methods in comparative plant ecology.* Chapman and Hall, London. 199-202pp.

Thompson, K. and Grime, J.P., 1983. A comparative study of germination responses to diurnally-fluctuating temperature. *Journal of Applied Ecology*, 20: 141-156.

Thompson, K., Grime, J.P., Mason, G., 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature,* 267: 147-149.

Tilman, D., 1980. Resources: a graphical mechanistic approach to competition and predation. *American Naturalist*, 116: 362-392.

Timan, D., 1982. *Resource competition and community structure.* Princeton University Press, New Jersey, 296p.

Tilman, D., 1988. *Plant strategies and the dynamics and structure of plant communities.* Princeton University Press, Princeton, New Jersey, 360p.

Topp, G.C. 1993. Soil water content. In Carter, M.R. (Ed) *Soil sampling and methods of analysis*, Canadian society of soil science, Lewis pub. 541-557pp.

Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 1990. The potential for ecological restoration in the Mercury islands. *In* Towns, D.R., Daugherty,C.H., and Atkinson,I.A.E. (Eds.) *Ecological restoration of New Zealand islands. conservation Sciences publication,* Department of conservation, Wellington. No.2: 91-108pp.

Turner, J.H., 1934. The viability of seeds. Bulletin of miscellaneous information. *Kew*, 6: 257-269.

Turner, N.C. and Jones, M.M., 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. *In* Turner, N.C. and Hramer, P.J (Eds.*) Adaptation of plants to water and high temperature stress*, Wiley, New York, 87-103pp.

Tylkowski, T., 1982. Thermal conditions for the pressiowing treatment of European elder and red elder. *Arboretum Kornickie*, 27: 347-355.

Ungar, I.A. and Woodell, S.R.J., 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. *Journal of Vegetation Science*, 4: 531-536.

United States National research council., 1974. *Rehabilitation potential of Western coal lands.* Balling Publishing Company, Cambridge, Massachusetts.

Valk, A.G. van der., 1981. Succession in wetlands: a Gleasonian approach. *Ecology,* 62: 688-696.

Van Hulst, R., 1987. Invasion models of vegetation dynamics. *Vegetatio*, 69: 123-131.

Viereck, L. A., 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Aleska. *Ecological Monograps*, 36: 181-199.

Vitousek, P.M. and Matson, P.A., 1985. Disturbance, nitrogen availability, and nitrogen loss in an intensively managed loblolly pine plantation. *Ecology,* 66: 1360-1376.

Vitousek, P.M. and Walker, L.R., 1987. Colonization, succession and resource availability: Ecosystem-level interactions. *In* Gray, A.J., Crawley, M.J., Edwards, P.J (Eds.) *Colonization, Succession and stability,* 26 th Symposium of the British Ecological Society, Blackwell Scientific Pub, London, 207- 223pp.

Voyce, M.I., 1998. *Elder (Sambucus nigra) as a facilitator of succession, Hoon Hay Valley, Banks Peninsula, New Zealand.* M.Sc. thesis, Lincoln University, New Zealand.

Wali, M.K., 1987. The structure, dynamics and rehabilitation of drastically disturbed ecosystems. *In* Khoshoo, T.N. (Ed.) *Perspectives in environmental management*, Oxford & IBH publications, New Delhi, India. 163-183pp.

Wali, M.K., 1992a. Ecology of the rehabilitation process. *In* M.K.Wali (Ed) *Ecosystem rehabilitation: Vol 1: Policy issues.* SPB Academic Publishing, The Hague, The Netherlands, 3-23pp.

Wali, M.K., (Ed.) 1992b. *Ecosystem rehabilitation vol. 2: Ecosystem analysis and synthesis.* SPB academic publishing, The Hague, The Netherlands.

Walker , T.W and Syers, J.K., 1976. The fate of phosphorus during pedogenesis. *Geoderma,* 15:1-19.

Waloff, N., 1968. Studies on the insect fauna on Scotish broom *Sarothamnus scoparious. Advances in EcologicalRresearch*, 5: 87-208.

Wang, D., Bachelard, E.P., Banks, J.C.G., 1988. Growth and water relations of seedlings of two subspeices of Eucalyptus globulus. *Tree Physiology,* 4: 129-138.

Wardle, J.A., 1984. *The New Zealand Beeches. Ecology, utilization and management.* New Zealand forest Service, Christchurch, 447p.

Waring, R.H and Schlesinger, W.H., 1985. *Forest economics: concepts and management.* Academic Press, Orlando, FL, 340p.

Webb, C.J., Sykes, W.R., Garnock-Jones.P.J., 1988. *Flora of New Zealand.* Vol. 4, DSIR, Christchurch, New Zealand.

Webb, C.J., Johnson, P., Sykes, B., 1990. *Flowering plants of New Zealand.* New Zealand, DSIR, The Caxton Press, 146p.

Werner, P.A and Platt, W.J., 1976. Ecological relationships of co-occurring goldenrods (Solidago:Compositae). *American Naturalist*, 110: 959-971.

Westoby, M., Leishman, M and Lord, J., 1996. Comparative ecology of seed size and dispersal. *Biological sciences*, Philosophical transactions of the royal society of London,. 351(1345): 1309-1318.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon,* 21:213-235.

Whittaker, R.H and Levin, S.A., 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology,* 12: 117-139.

Wieland, W.E and Bazzaz, F. A., 1975. Physiological ecology of three co-dominant successional annuals. *Ecoogy,* 56: 681-688.

Williams, B., 1993. *Biostatistics: concepts and applications for biologists*, Chapman and Hall, London, 105-106.

Williams, P.A., 1981. Aspects of the ecology of broom in Canterbury, NZ. *New Zealand Journal of Botany,* 19:31-43.

Williams, P.A., 1983. Secondary succession on the Port Hills, Banks Peninsula, Canterbury, New Zealand. *New Zealand Journal of Botany*, 21:237-247.

Williams, P.A. and Buxton, R.P., 1989. Response to reduced irradiance of 15 species of native and adventive shrub and tree seedlings from Eastern Canterbury. *New Zealand Journal of Ecology.* 12:95-101.

Wilson, H.D., 1992. *Banks Ecological Region: Port Hills, Herbert and Akaroa Ecological Districts.* Protected natural areas program report. 21. Department of Conservation.

Wilson, H.D., 1993. Bioclimatic zones and Banks Peninsula. *Canterbury Botanical Society Journal,* 27: 22-29.

Wilson, H.D., 1994. *Stewart Island plants: Field guide.* Manuka Press, Christchurch, New Zealand, 528p.

Wilson, H. and Galloway, T., 1993. *Small-leaved shrubs of New Zealand.* Manuka Press, Christchurch, New Zealand, 305p.

Wingate, D.B., 1978. Excluding competitors from Bermuda Petrel nesting burrows. *In* Temple, S.A. (Ed.) *Endangered birds: management techniques for preserving threatened species,* University of Wisconsin Press, Madison.

Wingate, D.B., 1985. The restoration of Nonsuch island as a living museum of Bermuda's pre-colonial terrestrial biome. *In* Moors, P.J. (Ed.) *Conservation of Island birds,* I.C.B.P. technology publications. 3: 225-238.

Young, J.A and Young, C.G., 1986. *Seeds of wildland plants.* Timber Press, Portland, OR.

Zar, J.H., 1984. *Biostatistical analysis.* Prentice-Hall Inc, Englewood Cliffs, New Jersey, 718p.

APPENDIX-1

(N=210ppm P=31ppm)

Salt	ml/litre nutrient solution	ppm
1M KH_2PO_4	1	31=P 39=K
1M KNO_3	5	195=K 70=N
1M $Ca(NO_3)_2$	5	200=Ca 140=N
1M $MgSO_4$	2	48=Mg 64=S
	g/litre	1 ml of micro
H_3BO_3	2.86	nutrients is
$MnCl_2.4H_2O$	1.81	added to 1ml
$ZnSO_4.7H_2O$	0.22	of nutrient
$CuSO_4.5H_2O$	0.08	solution

(N=140ppm P=15.5ppm)

Salt	ml/litre nutrient solution	ppm
1M KH_2PO_4	0.5	15.5=P 19.5=K
1M KOH	5	195=K
1M $Ca(NO_3)_2$	5	200=Ca 140=N
1M $MgSO_4$	2	48=Mg 64=S
	g/litre	1 ml of micro
H_3BO_3	2.86	nutrients is
$MnCl_2.4H_2O$	1.81	added to 1ml
$ZnSO_4.7H_2O$	0.22	of nutrient
$CuSO_4.5H_2O$	0.08	solution

(N= 266ppm P=46.5ppm)

Salt	ml/litre nutrient solution	ppm
1M KH_2PO_4	1	31=P 39=K
1M KNO_3	5	195=K 70=N
1M $Ca(NO_3)_2$	5	200=Ca 140=N
1M $MgSO_4$	2	48=Mg 64=S
1M NH_4NO_3	2	56=N
$.5MCa_3(PO_4)_2$	0.5	15.5=P 30=Ca
	g/litre	1 ml of micro
H_3BO_3	2.86	nutrients is
$MnCl_2.4H_2O$	1.81	added to 1ml
$ZnSO_4.7H_2O$	0.22	of nutrient
$CuSO_4.5H_2O$	0.08	solution

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1M $MgSO_4$	2	48=Mg 64=S
.5M Ca3(PO4)2	0.5	15.5=P 30=Ca
	g/litre	1 ml of micro
H_3BO_3	2.86	nutrients is
$MnCl_2.4H_2O$	1.81	added to 1ml
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1M $MgSO_4$	2	48=Mg 64=S
.5M $Ca_3(PO_4)_2$	0.5	15.5=P 30=Ca
	g/litre	1 ml of micro
H_3BO_3	2.86	nutrients is
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